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EVOLUTIONARY TRENDS IN THE GRASSES (POACEAE): A REVIEW

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INTRODUCTION

Poaceae (Gramineae) are one of the largest vascular plant families, containing between 650 and 785 genera, and 10,000 species (Clayton & Renvoize 1986; Watson 1990; Watson & Dallwitz 1992). Only Asteraceae (Compositae), Fabaceae (Leguminosae), and Orchidaceae contain more species than Poaceae (Watson 1990). Poaceae are also one of the most ecologically and economically important plant families (Thomasson 1987). Grasses and grasslands are distributed worldwide and account for 25–45% of the world's vegetation. Grasslands support diverse invertebrate and vertebrate communities (Hilu 1985), and are important elements in the development and stabilization of soil. Most human food comes directly or indirectly from grasses, either directly in the form of rice, maize, wheat, millet, and barley, or indirectly in the form of cows, sheep, pigs, and poultry raised on grasses or grains. Grasses have many other economically important uses, including bedding for humans and animals, thatch for mats and roofing, and reeds for fences, walls, and flooring. Bamboo is used as construction scaffolding in Asia.

Researchers have attempted to determine the origins of the Poaceae, and the evolutionary path that grasses have followed in becoming one of the dominant plant families on Earth. This paper will describe what has been learned to date about grass evolution.

PHYLOGENETIC ORIGINS

The evolutionary origin of the grasses is uncertain, obscured by the lack of unambiguous links between Poaceae and other monocotyledons (Clayton & Renvoize 1986; Stebbins 1987). Morphological similarities between grasses and sedges (Cyperaceae) were once thought to reflect a close relationship between these families. However, plant taxonomists now attribute these similarities to convergent evolution, and place Poaceae and Cyperaceae in different orders (Dahlgren et al. 1985; Clayton & Renvoize 1986; Clifford 1987). The nearest liv-

ing relatives of the grasses are now thought to exist among either the Joinvilleaceae, Flagellariaceae, or Restionaceae (Clayton 1981; Clayton & Renvoize 1986; Stebbins 1987). The family Joinvilleaceae is the leading candidate, having been identified as a sister group to Poaceae (Soreng & Davis 1998). Similarities in certain chloroplast DNA sequences suggest that members of the genus *Joinvillea* (Joinvilleaceae) may be the plants most closely related to Poaceae (Davis & Soreng 1993).

Taxonomic evidence (Clayton & Renvoize 1986; Watson & Dallwitz 1992) and cladistic analysis (Kellogg & Campbell 1987; Davis & Soreng 1993) support the division of Poaceae into three evolutionary sub-groups. These groups are the Bambusoideae, the Panicoideae/Arundinoideae/Chloridoideae, and the Pooideae. The Bambusoideae retain the greatest collection of primitive characters, and are considered the ancestral grouping by most authorities. The Bambusoideae are thought to have originated in tropical forest-edge habitats, suggesting that Poaceae as a whole probably evolved from tropical forest-edge species (Clayton & Renvoize 1986; Stebbins 1987; Renvoize & Clayton 1992).

From this presumptive forest-edge origin, grasses evolved along three different developmental trajectories, each adapted to a different general habitat type. The Bambusoids evolved to become tropical forest inhabitants, the Panicoids, Arundinoids, and Chloridoids occupied open savannas and warm prairies, and the Pooids became adapted to cool-temperate habitats (Renvoize & Clayton 1992). The grasses have adapted most successfully to open habitats, particularly habitats impacted by grazing, fire, and drought (Stebbins 1981; Coughenour 1985; Renvoize & Clayton 1992).

FOSSIL RECORD

While a late Cretaceous origin (more than 63 million years ago = >63 MYA) of the family is still debated (Takhtajan et al. 1963, in Daghlian 1981; Linder 1987; Stebbins 1987; Crepet & Feldman 1991), there is ample fossil evidence that grasses had evolved as a distinct taxonomic group by the Eocene epoch, 40–60 MYA (Daghlian 1981; Stebbins 1981; Clayton & Renvoize 1986; Thomasson 1987; Renvoize & Clayton 1992). Grass fossils have been found in African and South American Eocene formations (40–60 MYA), and in Eurasian (12–18 MYA) and North American (15–25 MYA) Miocene deposits (Clayton 1981; Daghlian 1981; Stebbins 1981; Coughenour 1985; Thomasson 1985; Stebbins 1987; Thomasson 1987; Crepet & Feldman 1991). Reports of Cretaceous grass fossils are considered erroneous, the result of specimen misidentification or misclassification (Thomasson 1980).

Early attempts at fossil grass classification were hampered by a poor understanding of taxonomic relationships among living grasses, and the depauperate fossil floras on which these classifications were based (Thomasson 1980). The prevalence of parallel evolution within the family also hindered the proper classification of both living and fossil grass species (Clayton & Renvoize 1986; Stebbins 1987). Compounding the problem was the fact that fossil grass pollen,

while distinctive at the family level, was of very little use in distinguishing among grass genera or species (Thomasson 1980).

While there are no clear fossil links between the grasses and other monocot families, careful examination of the available fossil record has improved our taxonomic understanding of Poaceae. Changes in fossil floral structures support the hypothesis that the hardened lemma and palea of certain North American grass species co-evolved with mammalian and/or invertebrate herbivores (Thomasson 1985; Thomasson 1987). These structures are thought to have evolved to increase the chances that a seed would survive mastication and passage through a herbivore gut (Thomasson 1985). Comparison of microscopic morphological characters such as phytoliths and micro-hairs helped clarify taxonomic relationships among fossil grasses (Thomasson 1987). Similarly, the discovery of Kranz anatomy in certain fossil grasses increased our understanding of relationships among fossil and living grasses. Kranz anatomy, which first appeared in Miocene (ca. 25 MYA) grass fossils (Thomasson 1987; Hattersley & Watson 1992), is a distinct and easily identified arrangement of photosynthetic bundle sheath cells, and is diagnostic for the C₄ (Hatch-Slack) carbon fixation pathway. C₄ physiology is a taxonomically important trait because C₄ grasses only occur in the warm prairie and savanna-adapted Panicoideae, Arundinoideae, and Chloridoideae. C₄ physiology is not found in the tropical forest-adapted Bambusoideae or cool temperate-adapted Pooideae (Clayton & Renvoize 1986).

EVOLUTIONARY DIVERSIFICATION

Diversification occurred as grasses adapted to life in open terrestrial habitats (Clayton 1981; Renvoize & Clayton 1992). Key adaptations arising during diversification included the reduction in size and number of floral parts, the development of wind pollination, and morphological and physiological adaptations that allowed grasses to tolerate and even benefit from grazing pressure, fire, and drought (Stebbins 1981; Clayton 1981; Connor 1981; Coughenour 1985).

Floral and reproductive evolution

Analysis of living and fossil floral morphology supports the hypothesis that grass flowers evolved by reduction (Clifford 1961; Connor 1981; Stebbins 1981). The modern grass flower (floret) is typically wind pollinated and composed of three stamens, two stigmas, and a single-chambered ovary with two lodicules at its base. These structures are covered and protected by the lemma and palea until the flower opens (Clayton 1990). One or more florets attached to the same stalk (rachilla) and subtended by a pair of bracts (glumes) comprise a spikelet, and one or more spikelets comprise an inflorescence. By contrast, the primitive grass flower was insect pollinated and had three bracts, three lodicules, six stamens, three stigmas, and a one- to three-chambered ovary (Clifford 1961; Connor 1981).

Floral reduction is associated with the transition from insect to wind pollination (Clifford 1961). In the grasses it involved the reduction of stamen numbers

from six to three, two, or one, stigma numbers from three to two or one, and the reduction of the perianth (petals and sepals, collectively) to one to three small lodicules (Clifford 1961). Large, showy flowers, which function to attract pollinators, require a substantial energy expenditure to construct and maintain. Such attractants are not needed in wind-pollinated plants, and so are often greatly reduced or completely absent (Mauseth 1988). In this way, floral reduction resulted in a large energy savings for any species achieving it. The energy saved could be channeled into other maintenance or survival functions. However, while solving one set of problems, floral reduction created a different set of potential problems in grasses.

Small flowers make small targets for wind-borne pollen. In addition, grass pollen is the shortest-lived pollen among the angiosperms (Clayton & Renvoize 1986). While sometimes carried long distances by the wind, grass pollen is viable for only a few hours, resulting in an effective pollination range of a few tens of meters under most circumstances (Clayton & Renvoize 1986). Further, grass flowers open for only 2–3 hours when they do flower, perhaps to minimize the introduction of pathogenic fungal spores during anthesis (Clayton & Renvoize 1986). These factors all reduce potential pollination success.

The grass inflorescence may have evolved to compensate for the reduction in the number of stamens and stigmas found in individual grass flowers (Clifford 1961). An inflorescence presents many more flowers, and a larger total cross-sectional area, to the wind than one individual flower could present. This increases the opportunity for wind-borne pollen grains to encounter a receptive stigma.

Other reproductive adaptations found in grasses include the development of cleistogamy (self-fertilization prior to, or in place of, flower opening) and apomixis (parthenogenic development of an unfertilized embryo) in some grasses, and a marked increase in vegetative propagation among many grass species (Clifford 1961). Cleistogamy, which occurs in at least 300 grass species (Clayton & Renvoize 1986), provides some opportunity for genetic recombination, though only through meiotic cross-over events. Apomixis, like vegetative propagation, is a form of asexual reproduction, producing offspring genetically identical to the parent (clones). While of little utility to fertile diploid individuals, apomixis may benefit polyploid species. Polyploidy often produces chromosomal mis-matches that result in partial or complete sterility. Apomixis may increase the prospects of successful reproduction in such species (Renvoize & Clayton 1992). Vegetative and apomictic clones can be at a competitive disadvantage when facing rapidly changing environmental conditions. However, like their parents, they are often very well suited to local conditions, a potential advantage when the habitat is stable and competition is fierce.

Co-evolution with herbivores

The co-evolution of grasses and grazing vertebrate herbivores was another important factor in grass evolution (Clayton 1981; Stebbins 1981). Grasslands and the hypsodont tooth first appeared in the fossil record about 60 MYA, during the Eocene (Stebbins 1981; Coughenour 1985). Since that time, grasses

evolved basal and intercalary meristems, a hardened lemma and palea to protect ingested seeds, and rhizomatous, trample-resistant sod. Grasses also shed the ability to produce defensive secondary metabolites (e.g., tannins, alkaloids) during this period. These co-evolutionary adaptations permitted horse-like mammals to utilize grasses as food, and grasses to thrive under a grazing regime that suppressed competing plant species (Clayton 1981; Stebbins 1981).

Coughenour (1985) noted that grasses existed as a distinct taxonomic group for "quite some time" before abundant grazers appeared, and has suggested that the adaptations attributed to grazing could have arisen in response to drought, competition, or the need for physical support rather than in response to grazing pressure. Nonetheless, the major grass adaptations attributed to grazing pressure appeared in the fossil record at about the same time as did vertebrate adaptations associated with a grazing habit (Stebbins 1981; Thomasson 1987), leading most authorities to accept the co-evolution hypothesis (Clayton 1981; Stebbins 1987).

Fire adaptations

Fire was a factor in grass evolution even before the appearance of vertebrate grazers (Clayton 1981). Fire benefits grasses by killing taller competitors, maximizing the light and nutrients that grasses can obtain (Weaver 1968). Annual production of grass litter increases the frequency of grassland fires, which reduces the overall fuel load and the maximum temperature of a grassland burn. Cooler-burning fires are less likely to damage basal grass meristems and subterranean grass roots and rhizomes, permitting them to rapidly sprout after a fire, intercept light, occupy space, and recycle nutrients before competitors can become established (Weaver 1968).

Drought adaptations

The climate in African, South American, and North American grassland regions shifted from warm, humid sub-tropical conditions towards cooler, semi-arid conditions between 25–60 MYA, during the Oligocene and Eocene epochs (Stebbins 1981). Several grass adaptations suggest that this climatic shift influenced grass evolution. Grasses evolved an extensive network of highly ramified roots, allowing them to efficiently scavenge moisture from the soil. When available soil moisture was insufficient to support metabolic processes, above-ground grass stems and leaves died. Grasses survived these dry periods in underground buds on roots and rhizomes.

Grasses also evolved the C_4 carbon fixation pathway during this period. C_4 grasses have a much lower CO_2 compensation point, the point at which photosynthesis equals respiration, than C_3 grasses (C.P. equals 5 parts per million for C_4 grasses versus 50 parts per million for C_3 grasses). This means that C_4 grasses maintain higher CO_2 diffusion gradients into their leaves than C_3 grasses. This is important because higher gas diffusion gradients permit C_4 grasses to maintain relatively high photosynthetic rates with partially closed stomata. Plants transpire less water with partially closed stomata than they do with fully-opened stomata. Thus, the greater CO_2 diffusion gradient in C_4 grasses results in greater

water use efficiency in C₄ grasses compared to C₃ grasses; that is, C₄ grasses used less water per unit carbon fixed than C₃ grasses. Greater water use efficiency confers a competitive advantage to C₄ grasses in hot or dry habitats.

Other physiological adaptations confer competitive advantage to C₄ grasses in hot or dry habitats. The optimal temperature and light levels for photosynthesis are higher in C₄ grasses compared to C₃ grasses. C₄ grasses are better adapted than C₃ plants to open terrestrial areas where hot, dry conditions and/or frequent fires have eliminated tall woody competitors.

The evolution of the C₄ pathway was one of the key adaptations that allowed Poaceae to dominate dry savannas and open tropical plains (Renvoize & Clayton 1992). C₄ panicoid, arundinoid, and chloridoid grasses were competitively superior to C₃ bambusoid and pooid grasses in hot, dry climates with high ambient light levels. However, C₃ grasses can compete effectively with C₄ grasses in relatively cool, moist, low-light habitats. The C₃ grasses, better adapted to cooler, more mesic conditions, became common components of forest-edge vegetation, and the dominant plants of northern and southern cool-temperate plains (Renvoize & Clayton 1992).

The absence of C₄ species in the Bamboideoideae and Pooideae (Clayton 1981) and the morphological characteristics of known C₃-C₄ intermediates (Hattersley 1987; Hattersley & Watson 1992) support the hypothesis that C₃ tropical forest-edge grasses represent the ancestral condition in Poaceae (Renvoize & Clayton 1992).

Polyplody

Polyplody, the occurrence of more than two complete sets of chromosomes in a cell nucleus, has played an important role in grass evolution. Polyplody occurs more often in Poaceae than in any other angiosperm family, with perhaps 80% of grass species having undergone a ploidy change at some point in their evolution (Stebbins 1985). However, the degree to which polyplody has occurred in the grasses varies greatly among genera. Only 14% of species in the genus *Melica* have undergone a ploidy change, whereas 91% of all species in the genus *Stipa* have done so (Hunziker & Stebbins 1987).

Most plant polyploids are the product of sexually-functional non-reduced gametes (Harlan & de Wet 1975). Non-reduced gametes occur when homologous chromosomes pairs fail to separate during the final step of gamete formation, so the gametes carry a double complement of chromosomes. Fertile polyploids generally contain an even number of chromosome pairs (4n, 8n, etc.), though at least one fertile, permanent triploid grass species (*Andropogon ternatus*) has been documented (Hunziker & Stebbins 1987). The most common base chromosome numbers in Poaceae are 7, 9, 10, and 12, but base chromosome complements vary widely within the family, ranging from 2n = 6 in one *Iseilema* species to as high as 2n = 265 in *Poa litorosa* (de Wet 1987; Hunziker & Stebbins 1987; Stebbins 1987).

Polyplody occurs either between species by interspecific or intergeneric hybridization (allopolyploidy), or within a species when genetically differentiated sub-populations of that species come back into contact and hybridize (autopoly-

ploidy by "secondary contact," Stebbins 1985). Hybridization often induces sterility. However, a ploidy change can sometimes restore fertility to otherwise sterile intermediates by doubling the chromosome complement following a hybridization event (Stebbins 1956).

The competitive advantage conferred by a ploidy change was once thought to take the form of greater resistance to temperature extremes or drought, or an enhanced ability to colonize new habitats (Stebbins 1987). It is now known that the impact of a ploidy change can be less apparent, and that not all polyploids are competitively superior (Stebbins 1987). Chromosome doubling by itself does not necessarily confer increased fitness. The mutations and hybridization events that often accompany polyploidy, or the genetic reconfiguration that often follows a ploidy change, are generally responsible for improvements in fitness (Stebbins 1987).

To a lesser extent, grass evolution has involved karyotype evolution. Reciprocal translocation, accessory chromosome alteration, mutation of repetitive DNA sequences, and transposition have all been linked to differentiation among grass species (Flavel 1986; Hunziker & Stebbins 1987), and the integration of transposable elements has been identified as a potential locus of evolutionary novelty (Hunziker & Stebbins 1987).

CURRENT STATUS

Research continues into the origins of the grasses, and new avenues of inquiry are being explored as new methods of investigation become available. Knowledge of the evolutionary relationships among the grasses will improve as new fossils are found, and as microscopic examination of existing grass fossils proceeds (Thomasson 1987). However, significant progress in this direction awaits the discovery of fossil intermediates that clearly link grasses to other monocots.

Investigators are using biochemical techniques to study taxonomic and evolutionary relationships among the grasses (Hilu 1987; Kahler & Price 1987; Chapman 1992; Soreng & Davis 1998). Molecular biologists have developed powerful tools to study the nucleotide sequences of RNA, and the nucleotide and gene sequences of nuclear and chloroplast DNA of living taxa. Evolutionary relationships can be deduced by comparing selected nucleotide or gene sequences among taxa and assuming that greater similarity between the taxa reflects less evolutionary divergence between them. These analytical techniques are being applied to the study of evolutionary relationships among living grasses, and may represent the best hope for uncovering the origins of the family.

Cladistic analysis is also being applied to Poaceae to improve our understanding of grass taxonomy and evolution (Kellogg & Campbell 1987; Kellogg & Watson 1993; Soreng & Davis 1998). Traditional taxonomic methods are based on morphological similarities (petal number, stamen count, ovary position, etc.) among taxa. Cladistics examines evolutionary similarities to determine taxonomic relationships. In cladistic analysis, evolutionary relationships (phylogenies) are determined by the number of evolutionarily recent ("derived") traits

shared among taxa; the greater the number of shared derived traits, the closer the taxonomic relationship.

Cladistic methodology can be applied to many different types of data. Cladistics has been used to study morphological character sets (Baum 1987), and rates of evolution in nucleotide sequences in chloroplast DNA restriction sites (Davis & Soreng 1993) and nuclear ribosomal RNA (Hamby & Zimmer 1988). Cladistic studies have generally supported the conclusions drawn from taxonomic evidence about the evolutionary origin of the family (Kellogg & Campbell 1987; Davis & Soreng 1993; Soreng & Davis 1998).

SUMMARY AND CONCLUSIONS

Grasses evolved as a distinct taxonomic group in the late Cretaceous or early Tertiary period. While exact taxonomic relationships are not yet known, the nearest living relatives to Poaceae are thought to be in the Joinvilleaceae, Flaggellariaceae, or Restionaceae. Taxonomic evidence and cladistic analysis support the division of Poaceae into three evolutionary groups: the Bambusoideae, the Panicoideae /Arundinoideae /Chloridoideae, and the Pooideae, with the ancestral family line rooted in the Bambusoideae. Each of these groups evolved to become best adapted to a different set of environmental conditions, the bambusoids to tropical forests, the panicoids, arundinoids, and chloridoids to open savannas and warm prairies, and the poidoids to cool-temperate habitats.

The fossil grass record dates from the Eocene, but contains no direct evidence of the links between Poaceae and other monocotyledons. Careful examination of existing fossils has clarified taxonomic relationships among living taxa.

Key evolutionary adaptations in the grasses include the reduction in size and number of floral parts, the development of wind pollination, and morphological and physiological adaptations that allowed grasses to tolerate and even benefit from grazing pressure, fire, and drought. Polyploidy, which occurs more often in Poaceae than any other vascular plant family, has had a great impact on grass evolution.

While the origins of Poaceae are not yet known, the addition of molecular techniques and cladistic analysis to our research tool box offers hope that we will one day fully understand the taxonomic relationships and evolutionary origins of the grasses.

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REVIEW

CONTEMPORARY PLANT SYSTEMATICS. By Dennis W. Woodland. Third edition, 2000. Hard-cover; xiv + 570 pages. Andrews University Press, 213 Information Services Building, Berrien Springs, MI 49104-1700. Telephone 616. 471. 6134. ISBN 1-883925-25-8. \$64.99.

Plant taxonomy or systematics is an academic subject that may be taught in a number of ways. For each of these approaches, one or more suitable textbooks are available. Some plant taxonomy courses (such as the one I took at Iowa State almost 30 years ago) stress family recognition, teaching students the characteristics of major angiosperm families. Instructors of such courses might select *Guide to Flowering Plant Families* by Wendy Zomlefer (University of North Carolina Press, 1994). Such courses may have a strong phylogenetic focus, examining both the processes of evolution and the cladistic patterns of relationships they create. Instructors of such a course might select *Plant Systematics: A Phylogenetic Approach* by Walter Judd, Christopher Campbell, Elizabeth Kellogg, and Peter Stevens (Sinauer Associates, 1999). For other students, taking plant taxonomy means that much of their time will be spent collecting and keying out species of the local flora. In doing so, they might rely on a field guide such as *Gleason's Plants of Michigan* by Richard Rabeler (Oakleaf Press, 1998). Yet other instructors emphasize principles and methods, teaching students the kinds of

data and means of data analysis used to address taxonomic questions. A logical choice for such a course might be *Plant Taxonomy: The Systematic Evaluation of Comparative Data* by Tod Stuessy (Columbia University Press, 1990) and its companion exercise book *Case Studies in Plant Taxonomy* (1994).

But what about the instructor who wants to expose his or her students to *all* these aspects of plant systematics? What textbooks are available that combine these approaches in a balanced fashion? It's not a rhetorical question, as I have been searching for just such a book to use in my own course. I want a text that will give students a very broad overview of plant taxonomy in its entirety, a book that will help them understand that systematics is a dynamic, multi-faceted, highly synthetic discipline. It has been a challenge to find a textbook that can competently cover the diversity of topics on my syllabus; as noted above, most texts on the market emphasize one particular approach, and ignore or soft-pedal others. For this reason, it was with considerable interest that I picked up the latest edition of *Contemporary Plant Systematics* by Dennis W. Woodland. In the review that follows, I will evaluate Woodland's book in terms of how well it meets the needs of a broad-based plant taxonomy course. In doing so, I will indicate the chapters that seem germane for each of the major teaching approaches mentioned above.

The *de rigueur* introductory chapter is one of the book's few weak points. It does define a number of important basic terms, and comments on the nature and significance of systematics, but is far too brief. In introducing a probably unfamiliar subject to students, one must expound in some detail on its philosophical bases, as well as its relationship to science and society. Systematics is an extremely synthetic discipline, drawing data from disparate fields (morphology, phytochemistry, cytology, palynology, molecular biology, ecology, biogeography, etc.) and returning to them a rational classification and a standardized system of names. That single fact, which effectively makes systematics the "hub of biology," must be highlighted right up front in any plant taxonomy textbook.

The second chapter, also introductory in tone, is a wonderfully concise and clear explanation of scientific names and the rules that govern them. Specifically, each of the six Principles of the current *International Code of Botanical Nomenclature* (International Association for Plant Taxonomy, 2000) is explained and its implications illustrated by examples. The numerous Articles and Recommendation that make up the bulk of the *Code* are not detailed; that would be inappropriate in an introductory text. However, they are mentioned under the Principles to which they apply. Especially appreciated is the concluding section, which explains the *Code's* requirements for naming a newly recognized species. This section may be handily illustrated by any number of examples from the current literature.

With these preliminaries concluded, the author swings into a pair of chapters that will be useful for the plant identification component of the course. Chapter 3 deals with dichotomous keys. My one complaint here is that the focus is on how to *write* a key, rather than on how to *use* one. I have never been convinced that having beginning students create a key (often to hardware or other non-living objects) helps them understand how to utilize one effectively. Of course, no actual keys for the identification of plants are included; the book would then be far too provincial for our modern global market. It is necessary for the instructor to supplement the text with an appropriate field guide or manual. In doing so, Appendix II will be most helpful, as it provides a concise guide to floras and manuals of the entire world, organized geographically. Chapter 4 is an excellent compendium on plant collecting and herbaria. All aspects of the collection and preservation of botanical specimens is covered here in detail. Of special value for a class full of neophytes is a section on the proper handling of herbarium specimens to avoid damage.

The next five chapters pertain to family diversity. Unlike many textbooks emphasizing plant families, not only are the angiosperms covered, but also major pteridophyte (Chapter 5) and gymnosperm families (Chapter 6). Many will consider this a real plus. Following a comprehensive discussion of the terminology used to describe angiosperms (Chapter 7), a chapter each is devoted to the dicots (Chapter 8) and monocots (Chapter 9). Families of both temperate and tropical climes are included here, increasing the number of places in which it would be appropriate to market the book. Woodland wisely declines to adopt recent molecular-cladistic classifications as the basis for his discussion of angiosperm families. He rightly reasons that these nascent proposals are as yet too incomplete and too labile to foist on beginning students. Instead, he employs the stalwart Cronquistian system (outlined in detail in Appendix III), which has been the standard for teaching and many other purposes for the past two decades. Those seeking to give this portion of the course a more pro-

nounced evolutionary focus will want to include Chapter 12, "Contemporary Views on the Origin of Vascular Plants."

I really like the format employed in these chapters. Each family occupies a page unto itself. At the top is an illustration with dissections (by Anita Reiss). A succinct description follows, broken up into distinct boldly headed paragraphs: General Description, Leaves, Flowers (with the names of the four floral organs likewise highlighted), Fruit, Seed, Distribution, Economic Value, Classification, and (an interesting addition to the usual information provided by such works) Fossil Record. As such, each page provides an excellent thumbnail sketch of the family covered. The discussion is, of course, not as detailed as one would find in the Zomlefer text mentioned above. But it is eminently suited to the needs of a course in which family recognition is only one component of the syllabus. My sole complaint is with the line drawings, which are executed in a rather dark, heavy style that is aesthetically unappealing. Worse, some of the drawings are misleading or erroneous. I was shocked to see that the syngenesious anther tube, a diagnostic feature of the Lobelioideae, has been omitted from the drawing of *Lobelia* (Fig. 8.185f). Such problems are obviated in large measure by the compact disk that accompanies the textbook. *Photo Atlas of the Vascular Plants* by Michael Clayton (University of Wisconsin, second edition, 1998) contains 4700 color images that more than make up for any shortcomings in the drawings.

For the portion of the course dealing with the methods and principles of systematics, Chapters 10 and 13 are germane. The former gives an excellent overview of the historical development of classification, including a good summary of the phenetic and cladistic schools of classification. The latter chapter provides concise coverage of various kinds of data used by systematists: anatomy (by Nels Lersten); morphology (by Rolf Sattler); molecular biology, to include both secondary compounds and macromolecules (by Loren Rieseberg); palynology (by Cliff Crompton); biogeography and ecology (by Peter Holland); and cytology and genetics (by Woodland). The only discipline that seems missing is embryology, which has contributed much important data at higher levels of the taxonomic hierarchy. Again, while these discussions are not as detailed as those in the Stuessy book cited above, they are more than adequate for a broad survey course.

The remaining portions of the book cover a diversity of interesting and useful topics. Chapter 11 provides a thorough overview of taxonomic literature, with an emphasis on standard reference works and indices. Instructors who assign research papers to their students will find this chapter invaluable. Chapter 14 discusses conservation of biodiversity and endangered species. Included here is a discussion (by Ernest Small and Suzanne Warwick) of the relationship of genetic engineering to conservation, specifically the threat posed by transgenic organisms. Surely this controversial current topic may be used to generate some lively classroom discussion! Chapter 15 covers the role of botanic gardens in society, and includes an illustrated tour of major gardens around the globe. In an epilogue, we find a too brief discussion of the relevance of systematics to society, a topic that (as noted above) should have been discussed, and at greater length, in Chapter 1. It also includes a seemingly unique and most welcome section on job opportunities in plant systematics and information on the requisite qualifications. As one might expect, the book includes a detailed glossary and a comprehensive bibliography for each chapter.

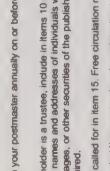
The book is generally well produced. Some typographical errors were noted: *Pilea* "pepperomoides" for *Pilea peperomoides* (pg. 4), "cladestic" for cladistic (pg. 109), *Himantoglossum hircinum* not italicized (pg. 492). A factual error (pg. 365): James E. Smith purchased the Linnaean herbarium for 1000 guineas, not (as stated) £1000. The guinea equalled 21 shillings, a pound sterling or sovereign just 20 shillings, so that the actual price paid was £1050.

After careful consideration, I have decided to adopt Woodland's book for classroom use next semester. It covers all areas that I feel a plant taxonomy course should cover, and there is nothing on my syllabus that it omits. Furthermore, depth of coverage of the various topics is entirely appropriate for an introductory course. All in all, it appears to me to be the single best textbook on the market today for courses that attempt to cover the entire breadth and depth of plant systematics. I only hope that my students will agree!

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On the cover: *Anemone canadensis* L. in Reeses Swamp,
near Burt Lake, Emmet County, MI.
Photographed by Marny Payne of Muncie, IN, 28 June 1987.

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EVIDENCE FOR A SPECIES-LEVEL DISTINCTION OF TWO CO-OCCURRING ASTERS: *ASTER PUNICEUS* L. AND *ASTER FIRMUS* NEES

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ABSTRACT

We examined the possibility that two co-occurring wetland asters, commonly referred to as *Aster puniceus* var. *puniceus* and *A. puniceus* var. *firmus*, are sufficiently distinct to be segregated at the species level. In our study of collected and field specimens we limited our research to 10 study sites in southern Michigan where both asters coexist. We assumed that if the two taxa belong to one species, gene flow (and hence, intermediate forms) will most likely occur in locations where they grow together (Wagner & Wagner 1983). By quantifying previously-cited characters and new comparative traits of below-ground parts, above-ground vegetative characteristics and capitulecence architecture, we found no evidence of intergradation between these coexisting populations. Therefore, we conclude that the most appropriate taxonomic treatment of these asters is to recognize a species-level designation: *Aster puniceus* L. and *Aster firmus* Nees.

INTRODUCTION

The notoriously difficult genus *Aster* has provided plant taxonomists fertile ground for inquiry and debate (Jones 1980a, 1980b, 1989; Nesom 1994; Semple et al. 1983, Semple et al. 1996; Shinners 1941, 1946; Van Faassen 1963; Wiegand 1924). Asa Gray, the renowned 19th century botanist, lamented,

I am half dead with *Aster* . . . If you hear of my breaking down utterly, and being sent to an asylum, you may lay it to *Aster*, which is a slow and fatal poison (quoted in Semple 1987).

Further illustration of the complexity and promiscuity of these taxa has been voiced by Dr. Arthur Cronquist:

If complete morphological discontinuity were the sole criterion for the acceptance of species in this group, they could all be reduced to one species (Cronquist 1943).

Such confusion is well represented in the swamp aster (*Aster puniceus* L.). *Aster puniceus* (sensu lato) is typically classified under the subgenus *Sympyotrichum* (Nees) A. G. Jones, section *Salicifolii* Torrey & A. Gray, and subsection *Leucanthi* (Nees) A. G. Jones (Jones 1980a). However, recent taxonomic work suggests the genus *Aster* be separated into 13 distinct genera and that the taxon of this study be classified within the newly proposed genus *Sympyotrichum* (Nesom 1994). However, since the foundational literature this study is based upon uses the

older nomenclature, and since the new work cited above has not been widely utilized to date, we will refer to the more traditional names in this paper.

Aster puniceus (sensu lato) is distinguished from other species of *Aster* by several characters: achenes with 3–5(6) ribs; leaves clasping, often strongly auriculate; principal cauline leaves sparsely toothed, gradually tapered toward the base; stem variably hispid; and phyllaries glabrous, eglandular and long-acuminate or attenuate.

When first named, this taxon was not described as exhibiting significant morphological variation. However, as variation has increasingly been recognized, two main subtaxa within *Aster puniceus* have been delineated. One, *A. puniceus* (sensu stricto) has densely hispid stems, purple ray flowers, and a widely spreading capitulecence. The other taxon (which has been variously named) tends to be less hispid, with white ray flowers and a more leafy, crowded capitulecence. Wiegand (1924) recognized the two types and segregated the smooth-stemmed *Aster* as a separate species, *Aster lucidulus* (Gray) Wiegand. However, this taxon had previously been named *Aster firmus* Nees; therefore, *A. firmus* should be the correct name for this taxon when segregated at the rank of species (Jones 1980b).

Yet, the greatest confusion involving these plants is not which species name is most appropriate for the smooth-stemmed *Aster*, but whether or not this taxon truly deserves species-level rank. Many taxonomists include both plants within *Aster puniceus*, recognizing the swamp aster as *A. puniceus* var. *puniceus*, and the smooth-stemmed aster as *A. puniceus* var. *firmus* (Nees) Torrey & A. Gray (Jones 1989, Semple et al. 1983, Semple & Heard 1987; Voss 1996). At least one author (Jones 1984) has separated the taxa at the subspecies level. Others recognize two species (Gleason 1952; Gleason & Cronquist 1991; Jones 1980a, 1980b; Shinners 1941, 1946; Wiegand 1924), while still others apparently make no distinction below the species level (Britton & Brown 1913; Chmielewski 1987; Semple 1980a, 1980b; Van Faasen 1971, Van Faasen & Sterk 1973).

Authors who do not recognize these two asters as separate species generally appeal to the presence of overlapping characters, suggesting this as evidence of intergradation or even complete lack of discontinuity (Jones 1989; Voss 1996). We evaluated many of these overlapping traits as well as some infrequently cited and novel characters from field and herbarium specimens to ascertain whether morphological discontinuity exists between these asters. Although we did not examine the type specimens, our designations are based upon and consistent with descriptions by Gleason (1952), Gleason & Cronquist (1991), Jones (1980a), Shinners (1941, 1946), Voss (1996), and Wiegand (1924).

We collected data from both herbarium and field specimens. While it is likely many of the herbarium specimens had come from sites where the two taxa do not co-occur, our field observations were done exclusively at sites where both asters are found in coexisting populations. We predicted that if the taxa are able to cross, introgression would most likely occur at these field sites where the plants exist in proximity (often within one meter of each other). If plants with intermediate traits were found at these locations, we would conclude that these are two varieties of one species. By contrast, if these asters clearly retain their distinctness while living in such proximity, we would conclude that no gene flow is occurring and a species-level designation is warranted (Wagner & Wagner 1983).

METHODS

For this investigation we collected specimens and directly examined living plants from several sites across southern Michigan and analyzed herbarium specimens at the University of Michigan Herbarium (MICH). A total of 22 *Aster puniceus* and 40 *A. firmus* plants were collected from co-occurring populations at seven sites across southern Michigan: Waterloo State Recreation Area (Washtenaw County), Pinckney State Recreation Area (Washtenaw County), Hadley Road (Washtenaw County), Furstenburg Park (Ann Arbor City Park, Washtenaw County), Ives Road Fen (Nature Conservancy Preserve, Lenawee County), Lost Nation State Game Area (Hillsdale County), and Bakertown Fen (Nature Conservancy Preserve, Berrien County). Plants were collected from September to November in 1993, 1994 and 1995. Specimens were pressed, dried, and later examined. Five voucher specimens were deposited at MICH (Warners *A. firmus* 747, 757, 758; *A. puniceus* 756, 745, MICH). All remaining specimens are retained at the Calvin College Herbarium in Grand Rapids, Michigan.

From the collected specimens we quantified rhizome length, leaf midvein pubescence and capitulecence structure, and used these data to graphically illustrate differences. Specimens were collected with as much below-ground material as possible so that various rhizome lengths could be assessed (see Figure 1). Midvein pubescence was measured by averaging hair counts per millimeter of midvein from three leaves per plant under a dissecting microscope. These measurements were taken from the abaxial surface of cauline leaves at an arbitrary location within 3 cm from the base of the leaf. To quantify differences in capitulecence architecture we created a variable, mean BRC (Branching Ratio in the Capitulecence). Mean BRC is the mean ratio of non-flowering to flowering segments (cm) on the three lowermost capitulecence branches (Figure 2).

We also gathered data from living plants in coexisting populations at Warren Townsend Park (Kent County), Pickerel Lake Nature Preserve (Kent County), Flat River State Game Area (Montcalm County), Waterloo State Recreation Area (Washtenaw County), Ives Road Fen (Lenawee County), and Bakertown Fen (Berrien County). Observations were made between 3 July and 30 August 1998. At these sites we collected data for three variables (stem thickness, number of shoots per plant and stem pubescence) from a total of 22 *Aster puniceus* and 28 *A. firmus* plants. Stem thickness was measured at a point 20 cm above the soil surface. The number of living shoots (current year) from the base of a plant was counted after sufficient surface soil was removed to confidently assess which shoots emerged from the same below-ground structure. Stem pubescence was measured by counting the number of hairs (per 25 mm²) on the stem at a point 60 cm above the soil surface.

To assess data from a broader geographical region than southern Michigan, 148 specimens of *Aster puniceus* and 68 specimens of *A. firmus* were examined at MICH by qualitatively evaluating four characters: pubescence in the capitulecence, stem pubescence, pubescence on abaxial surface of leaf midveins, and underground parts. A complete list of citations for each of these specimens may be requested from the authors.



FIGURE 1. Capitulescence and below-ground architectures of *Aster puniceus* (left) and *Aster firmus* (right).

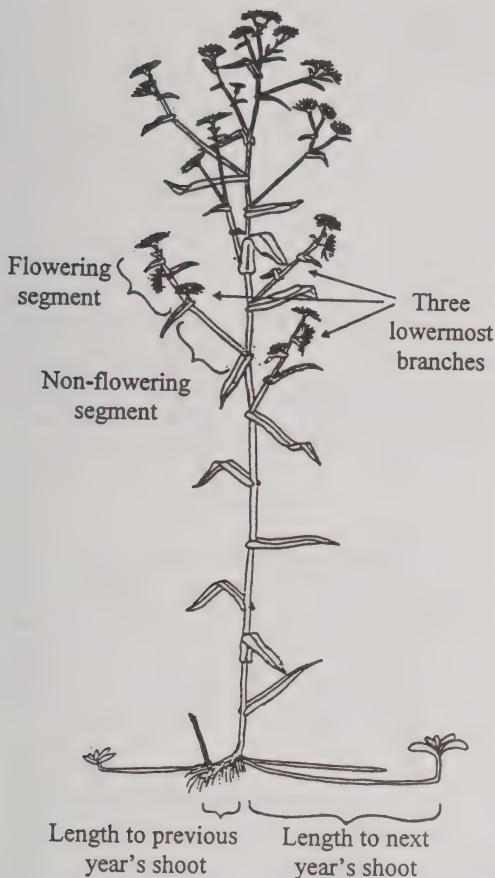


FIGURE 2. Diagram of various characters used to evaluate the two asters from collected specimens. Rhizome lengths were measured in centimeters and mean BRC was calculated by comparing the portions of the capitulose branches which were flowering and non-flowering (see text for detailed description).

Calculations were done with Microsoft Excel 5.0. The graphs and table were generated using Cricket Graph 1.3 and Microsoft Excel 5.0.

RESULTS

The specimens we collected from coexisting populations exhibited several distinct morphological traits. Figures 1 and 3 illustrate that *Aster puniceus* consistently emerges from a short caudex, while *A. firmus* annually spreads by extended rhizomes. Figure 4 graphically illustrates differences between the taxa using the variables maximum length to next year's shoot, mean BRC, and number of leaf midvein hairs (there are fewer specimens represented in the graphs than the total number collected because we only graphed those specimens that clearly illustrated all the characters analyzed in the graphs). Underground distance to the following year's shoot was always greater in *A. firmus* ($\bar{x} = 29.0$ cm, $sd = 26.6$) than in *A. puniceus* ($\bar{x} = 1.8$ cm, $sd = 1.3$). *Aster puniceus* was found

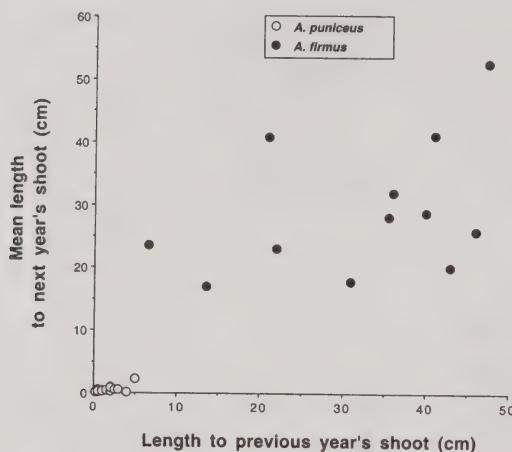


FIGURE 3. A comparison of below-ground structures of the two asters: length to previous year's shoot plotted against the mean length to next year's shoot.

to have variable numbers of cauline leaf midvein hairs ($\bar{x} = 6.8/\text{mm}$, $sd = 2.3$), while *A. firmus* midveins were typically glabrous ($\bar{x} = 0.14/\text{mm}$, $sd = 0.37$). The two anomalous individuals (one *A. puniceus* without hairs and one *A. firmus* with hairs) maintained other characters consistent with their taxon. Mean BRC was consistently lower in *A. puniceus* ($\bar{x} = 0.86$, $sd = 0.39$) than in *A. firmus* ($\bar{x} = 3.38$, $sd = 1.43$), indicating that the heads of *A. firmus* are much more crowded along the outermost part of the capitulecence.

Observations of living plants in the field yielded additional quantitative data that further delineate the two asters. Figure 5 illustrates these differences using the variables stem thickness (at 20 cm above the soil surface), number of shoots from the base of a plant, and number of stem hairs (per 25 mm^2 on the stem 60 cm above soil surface). *Aster puniceus* can grow in clumps of several shoots per plant ($\bar{x} = 2.4$, $sd = 1.6$), whereas we always found *A. firmus* shoots arising singly ($\bar{x} = 1.0$, $sd = 0$). *Aster puniceus* also commonly displays thicker stems ($\bar{x} = 7.2\text{ mm}$, $sd = 1.5$) than *A. firmus* ($\bar{x} = 4.0$, $sd = 0.93$) and the stems of *A. puniceus* are more densely pubescent ($\bar{x} = 15.7$, $sd = 4.5$) than are the stems of *A. firmus* ($\bar{x} = 2.3$, $sd = 1.9$).

The qualitative data gathered from specimens at MICH illustrate general trends in pubescence differences and further supported differences we had quantified from below-ground material. Four comparisons in pubescence patterns were made (Table 1). Stem and leaf pubescence occurred more commonly and at greater density in *Aster puniceus*. However, pubescence in the capitulecence was found in distinct lines more frequently in *A. firmus*.

We also attempted to compare below-ground material from the MICH specimens (Figure 6). Unfortunately, the majority of herbarium specimens (over 60%) did not include sufficient below-ground material to make such a comparison. However, of those with sufficient root material, the vast majority of *Aster puniceus* specimens exhibited a caudex, and nearly all *A. firmus* specimens had extended rhizomes.

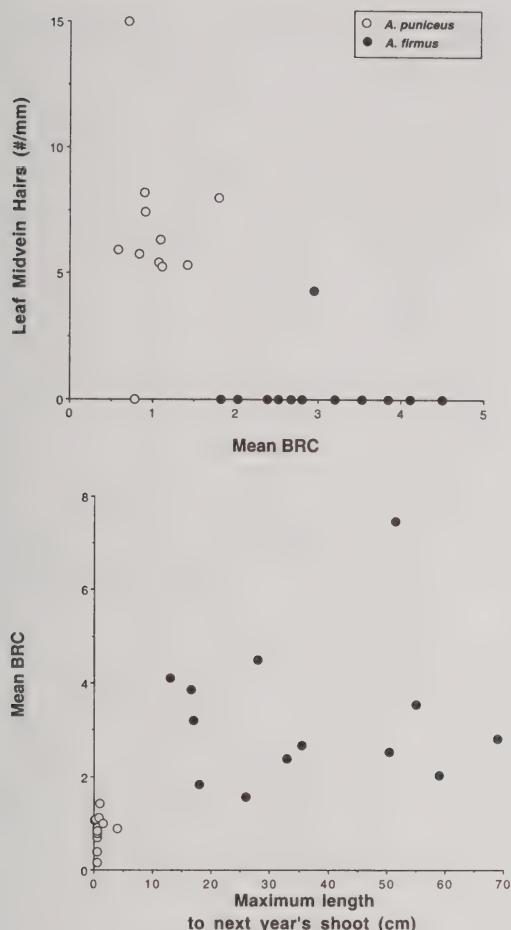


FIGURE 4. Evaluation of below-ground structure, mean BRC, and leaf midvein pubescence from collected specimens. (a) Mean branching ratio in the capitulecence plotted against mean number of hairs on abaxial caulin leaf midvein. (b) Maximum rhizome length to next year's shoot plotted against mean branching ratio in the capitulecence (see Methods).

DISCUSSION

In our evaluation of these plants we have followed two stated lines of advice offered for those who conduct taxonomic research within *Aster*. First, Gleason & Cronquist (1991) and others (Jones 1980b; Semple & Brouillet 1980a; Voss 1996) stress the importance of considering the entire plant body when generating keys or making identifications within this genus. Shinners (1941) has also raised this concern, emphasizing that "rootstocks are of critical importance." Second, since many of the species within *Aster* are so variable, it has been recommended to use a suite of characters to delineate species, rather than a single or limited number of traits (Carlquist 1976; Cronquist 1943; Semple & Brouillet 1980a).

Several of the traits we used (stem pubescence, capitulecence architecture, leaf midvein hairs) have been used qualitatively by other authors to suggest character overlap (Jones 1989, Voss 1996). However, by carefully quantifying these

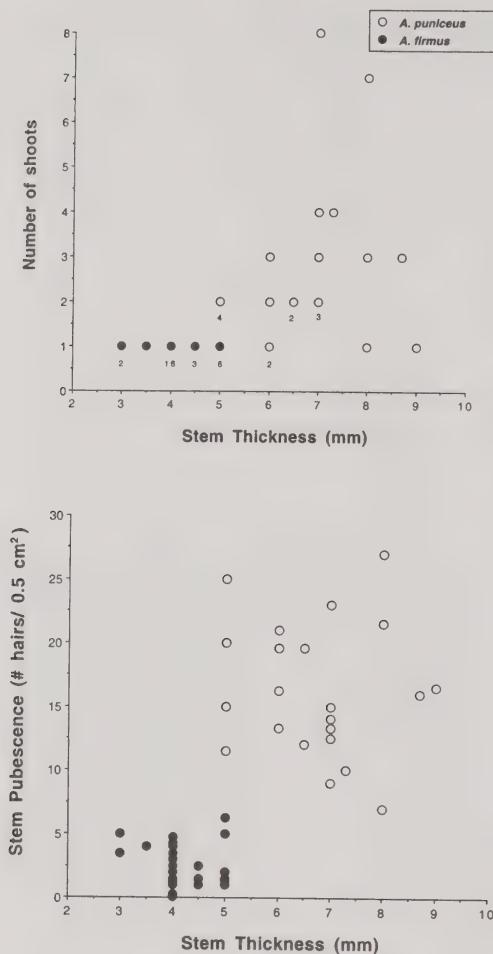


FIGURE 5. Evaluation of stem thickness, number of shoots and stem pubescence from living plants. (a) Stem thickness measured at 20 cm above the soil surface plotted against the number of shoots arising from the base of an individual plant. Points accompanied by numbers represent the number of individuals which shared identical values. (b) Stem pubescence measured at 60 cm above the soil surface plotted against stem thickness measured at 20 cm above the soil surface.

and other traits, we found little evidence of introgression, leading us to suggest these taxa should be classified as two distinct species. The differences we found are particularly noteworthy since we limited our quantitative comparisons to plants that were existing in overlapping populations. If the two *Asters* are of the same species, cross-fertilization and intermediate forms would be expected, especially in areas where the plants co-occur (Wagner & Wagner 1983). Yet we found no evidence that supports the existence of intermediate forms, even though all the plants we evaluated were from coexisting populations.

A comparison of below-ground structures of these *Asters* produced the most significant contrast. The stout caudex of *Aster puniceus* differs markedly from the extended rhizomes of *A. firmus*. We found that *A. firmus* shoots typically produce 2–6 rhizomes beginning in mid to late summer, each eventually reaching between 20–70 cm in length by late fall. To our knowledge these are the longest

rhizomes reported for any species of Michigan *Aster*. In late fall *A. firmus* rhizome tips generally form a leafy photosynthetic rosette at some distance from the "parent" shoot. Late season rosettes are also formed in *A. puniceus*, but due to the absence of rhizomes, they are always found at the immediate base of the current year's shoot.

This important difference deserves emphasis because it likely influences other morphological traits, including two of our variables, stem thickness and number of shoots at the base of a plant. Although we did not measure stored energy, we predict the type of perennating below-ground structure influences the thickness of a shoot as well as the number of shoots arising at a given point. For instance, while the extended rhizome of *Aster firmus* generally supports only one slender shoot, the stout caudex of *A. puniceus* can support multiple and larger shoots.

These contrasting below-ground structures also give rise to significant ecological differences. Each shoot of *Aster firmus* produces 2–6 new vegetative shoots each generation via extended rhizomes. This means of reproduction allows *A. firmus* to increase in abundance and spread across a suitable habitat during a relatively short time period, even occasionally spreading into drier upland soils. The ability to expand clonally may be a primary reason why *A. firmus* can achieve much higher relative abundance than *A. puniceus*, to the point of being the dominant forb species in some herbaceous wetland communities (Jones 1980b, 1989; Shinners 1946; Voss 1996; Warners 1997).

By contrast, *A. puniceus* populations are generally comprised of a few distinct individuals, each of which may consist of several shoots, always found in wet, organic soils. While these clumps will slowly increase in size, the increase is very slow and each clump remains stationary, occupying the same immediate location throughout its lifetime. The lower relative abundance of *A. puniceus* compared with *A. firmus*, as well as its more restricted habitat requirements, are likely related to its limited ability to disperse via vegetative propagation.

Specimens from MICH demonstrate that below-ground material is often neglected when collecting these plants. The rhizomes of *Aster firmus* are particularly difficult to remove from the dense sedge meadow root mat in which they typically grow. Since most taxonomic work relies heavily on herbarium specimens, it is not surprising that below-ground structures of these plants have largely been overlooked, and to our knowledge never before quantified.

Other above ground characteristics also help to separate these two asters. Several authors have commented on the more compact, leafy capitulecence of *Aster firmus* and the more open, less leafy capitulecence of *A. puniceus* (Jones 1980b, 1989; Shinners 1941; Wiegand 1924). Our variable, mean BRC, is the first quantitative description of these contrasting capitulecence architectures. The combinations of a long rhizome with a compact capitulecence in *A. firmus* and a short caudex with an open, lax capitulecence in *A. puniceus* is striking and indicates these two characters likely have a different genetic basis (Brouillet, personal communication).

An infrequently cited character, leaf midvein pubescence (but see Voss 1996), also consistently separates the two species. Stem pubescence is a commonly cited character in comparing these two asters, but many authors have noted how variable this trait can be. We concur that stem pubescence in these taxa is vari-

TABLE 1. Values indicate the percentage of plants that exhibited each trait except for "pubescence on stem," which was scored as either dense or sparse.

Pubescence	<i>A. puniceus</i>	<i>A. firmus</i>
On midvein of cauline leaf	91%	30%
On the stem	80%, dense	85%, sparse
On midvein of capitulecence leaf	80%	13%
In lines in capitulecence	28%	77%

able, yet when we standardized stem pubescence by quantifying stem hairs at a point 60 cm above the soil surface on mature individuals, *A. puniceus* was found to have consistently higher values than *A. firmus*. Stem pubescence is commonly used to compare these plants, and it has been cited both in support of a species-level rank (Jones 1980b; Shinners 1941, 1946) and as evidence for intergradation (Jones 1989; Semple et al. 1983). This and other often cited overlapping characters (such as ray flower color, head size and habitat preference) are not surprising, given the high variability within many species of *Aster* and the apparently close relationship of these two taxa. These characters illustrate the confusion that can arise when a limited number of morphological traits from a limited portion of the plant body are utilized. We have found stem pubescence to be an important comparative trait, but suggest that it be carefully quantified and used in conjunction with a suite of other characters.

In summary, by standardizing and quantifying traits that previously have been only qualitatively described and by evaluating new characters we find a clear discontinuity between plants here referred to as *Aster puniceus* and *A. firmus*. Our data show clear segregation based upon several unrelated characters and do not support the presence of intermediate forms even though all the plants used in our quantitative analyses were collected from coexisting populations (Wagner &

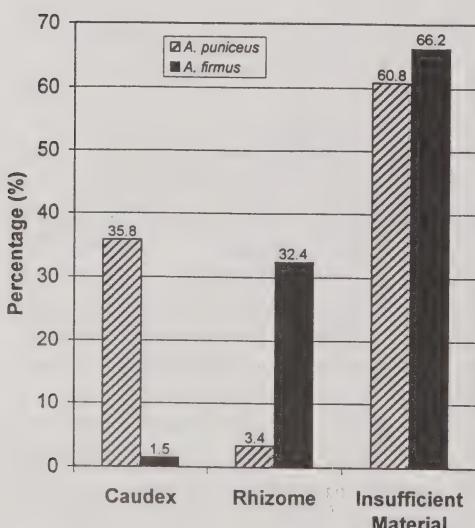


FIGURE 6. Comparison of underground perennating structures from *Aster puniceus* (n=148) and *A. firmus* (n=68) specimens held in MICH. Rhizomes were defined as horizontal stems greater than 5 cm in length. Plants listed in the "insufficient material" category either had no below-ground material or the parts were too incomplete to assess.

Wagner 1983). We conclude that the most appropriate taxonomic treatment of these two asters is a species-level separation.

This study also identifies the need for additional research on these taxa. Our interpretation of the numerous treatments which have failed to recognize a species-level distinction is that a few overlapping characters (stem pubescence, ligule color, and habitat) have been emphasized, while other more definitive characters (particularly below-ground structures) have been overlooked. However, we acknowledge the possibility that these asters behave as distinct species in a portion of their range (including southern Michigan), but may intergrade in other areas, as reported by Jones (1984). Our assessment of herbarium material did not support this phenomenon, but future quantitative research on populations outside the range covered in this study will more confidently evaluate this possibility. Further research that assesses phenotypic plasticity (possibly with additional characters such as capitulecence bract size, capitulecence bract biomass, floral characters, involucral bract traits, etc.) using controlled pollination experiments, as well as molecular techniques, will also contribute to a more detailed understanding of the relatedness of these two asters.

KEY TO ASTER PUNICEUS AND A. FIRMUS

1. Stems densely pubescent, usually purplish; abaxial caudine leaf midvein moderately to densely pubescent; capitulecence widely spreading and heads with lavender to purple ray florets; shoots often found in clumps of 2–6 arising from a persistent stout caudex *Aster puniceus*.
1. Stems glabrous, occasionally hispidulous in lines; abaxial caudine leaf midvein glabrous; capitulecence dense, leafy; heads with white to pale lavender ray florets; shoots arising singly from elongate rhizomes *Aster firmus*.

DESCRIPTIONS OF THE SPECIES

Aster puniceus L. Sp. Pl. 875. 1753.
'Swamp Aster,' 'Purple-stemmed Aster'

Herbaceous perennial with several new shoots emerging annually from a single stout caudex. Stems relatively broad near base (5–11 mm diameter), erect, 50–200 cm tall, usually uniformly anthocyanotic (Semple & Heard 1987). Pubescence on stem densely hirsute, 10–30 hairs per 25 mm²; pubescence in capitulecence moderately dense, occasionally in lines decurrent from nodes. Leaves of winter-rosettes large (Jones 1980b; Gleason and Cronquist 1991), basal leaves commonly deciduous at anthesis. Cauline leaves alternate, 10–22 cm long, 3–4 cm wide at widest point, dark green (Semple 1983), margins crenate-serrate, elliptic to oblanceolate, auriculate clasping; abaxial midvein moderately to densely hispid (5–10 hairs/ mm near leaf base). Capitulecence open, lax, paniculiform with widely spreading heads. Leaves in capitulecence

sparse and abruptly reduced in size (50% to 25% size of caudine leaves). Capitula 2–3.5 (4) cm in diameter with rays fully extended. Involucel campanulate, (6) 8–12 (15) mm long (Jones 1989), typically not graduated. Phyllaries slender, long-attenuate, 6–10 (15) mm long, flexible, herbaceous. Ray florets 20–40 (to 60), 12–18(20) mm long, lavender to purple. Disk florets 30–50, narrow but dilated at throat, (4.5) 5–6 mm long, limb turning from cream or yellow to pink or purple after anthesis. Achenes obconic, (2) 2.5–3.5 (4) mm long and 1 mm or less across, 1 rib per side. Pappus a single, simple whorl.

Flowering (late August) September–October. Fruiting October–November. Range extending southward from northeastern states along the Appalachian mountains to Georgia, northwest into Alberta and westward to Nebraska (Semple 1983); most abundant in the eastern part of its range (Semple 1987). Habitat predominantly open to moderately shaded, very wet peat substrate.

Aster firmus Nees. Syn. Ast. 25 (1818).

Syn. *Aster lucidulus* (Gray) Wiegand. *Rhodora* 26: 4 (1924).

‘Smooth-stemmed Aster’

Herbaceous perennial spreading clonally, often forming large colonies. New shoots emerging singly from long, strongly creeping rhizomes (to 70 cm long). Stems moderately thin at base (2–8 mm diameter), erect, 50–200 cm tall, anthocyanotic directly above each node. Basal stem portions often hispidulous, but upper stem (> 30 cm above ground) glabrous with occasional hairs found in decurrent lines from nodes. Leaves of winter rosette small, basal leaves deciduous at anthesis. Cauline leaves alternate, 5–15 cm long, 2–3 cm wide at widest point, typically light green, oblanceolate, auriculate clasping; abaxial midvein glabrous, occasionally hispidulus near tip. Capitulecence densely paniculiform to corymbiform with crowded heads. Leaves in capitulecence slightly and gradually reduced in size from caudine leaves, crowded, at times overtopping heads. Capitula 1.5–3.5 cm in diameter with rays fully extended. Involucel campanulate 6–10 mm long, somewhat graduated. Phyllaries often acute, not strongly attenuate, 6–10 mm long, flexible, herbaceous. Ray florets 20–40, 10–18 mm long, white to pale lavender. Disk florets 30–50, narrow but dilated at throat, (4.5) 5–6 mm long, limb turning from cream or yellow to pink or purple after anthesis. Achenes obconic, 1.7–3.0 mm long and 1 mm or less across, 1 rib per side. Pappus a single, simple whorl.

Flowering Early September–October. Fruiting October–November (Jones 1980b, 1989). Range extending southward from northeastern states along Appalachian mountains to Georgia, northwest into Alberta and westward to Nebraska (Semple 1983); more common in the western part of range (Semple 1987). Habitat predominantly open, wet ground, but prone to spread into mesic mineral soils.

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David P. Warners and Daniel C. Laughlin

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On the cover: *Cardinal-flower*, *Lobelia cardinalis* L., photographed at
the University of Michigan Biological Station, summer 1987,
by Marny Payne, 800 West Charles, #2, Muncie, Indiana 47305.

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REDISCOVERY OF *RHYNCHOSPORA (PSILOCARYA) NITENS* (CYPERACEAE) IN THE GREAT LAKES REGION.

A.A. Reznicek

University of Michigan Herbarium
North University Building
Ann Arbor, Michigan 48109

Rhynchospora nitens (Vahl) A. Gray is a sedge of primarily southern coastal plain distribution in the United States, occurring eastwards from Texas along the Gulf coastal plain, and then northwards along the Atlantic coastal plain to Massachusetts. It has also been recorded as a coastal plain disjunct in the Great Lakes region in northwest Indiana (Pepoon, 1927; Peattie, 1930; Deam 1940). Southward, *R. nitens* occurs in the tropics through the Caribbean and into Central America (Thomas, 1994). *Rhynchospora nitens* and related annual species such as *R. scirpoides* (Torr.) Griseb. and the primarily tropical *R. eximia* (Nees) Boeck. have in the past sometimes been recognized as the genus *Psilocarya* (Fernald, 1950; Voss, 1972; Swink & Wilhelm, 1994), but almost all authors now subsume them into a more broadly circumscribed *Rhynchospora* (Tucker, 1987; Bruhl, 1995; Goetghebeur, 1998).

Rhynchospora nitens, however, is very rare in the northern portions of its range. In New England, it was rediscovered after a hiatus of half a century (Sorrie 1977), and there had been only one prior collection. In the Great Lakes region, until this discovery, it was last recorded in 1899 in Porter County, Indiana and thought to be "now possibly extirpated in the Chicago region" (Swink & Wilhelm, 1994). It was then one of only two species of coastal plain disjuncts in the Great Lakes region that had not been collected in this century, the other being *Limnobium spongia* (Bosc) Steud. (Reznicek, 1994).

The species was rediscovered in the Great Lakes region, and also added to the flora of Michigan on 18 August 1999 at Goose Lake in Allegan County. The summer and fall of 1999 provided an excellent opportunity for searching for plants occurring on drawn down lake and pond shores, including many coastal plain disjuncts, because of the generally low water levels throughout the Great Lakes region. Goose Lake, like some other small, very shallow, and nearly flat-bottomed lakes, was completely drawn down, the bottom being a peaty and sandy meadow dominated by species characteristic of such draw down habitats, including extensive, colorful stands of *Rhexia virginica* L., *Panicum* spp., *Polygonum* spp., *Rhynchospora macrostachya* A. Gray, and *R. capitellata* (Michx.) Vahl, and numerous other forbs and graminoids. *Rhynchospora nitens* was abundant in the central areas of the lake bottom, forming a continuous colony acres in size with many thousands of plants. At this site, *R. scirpoides* (Reznicek 10967, MICH) was also present and reasonably frequent, but occurred primarily around the margin of the lake and less commonly throughout the lake bottom. A number of other similar sites in southwestern Michigan were examined after this

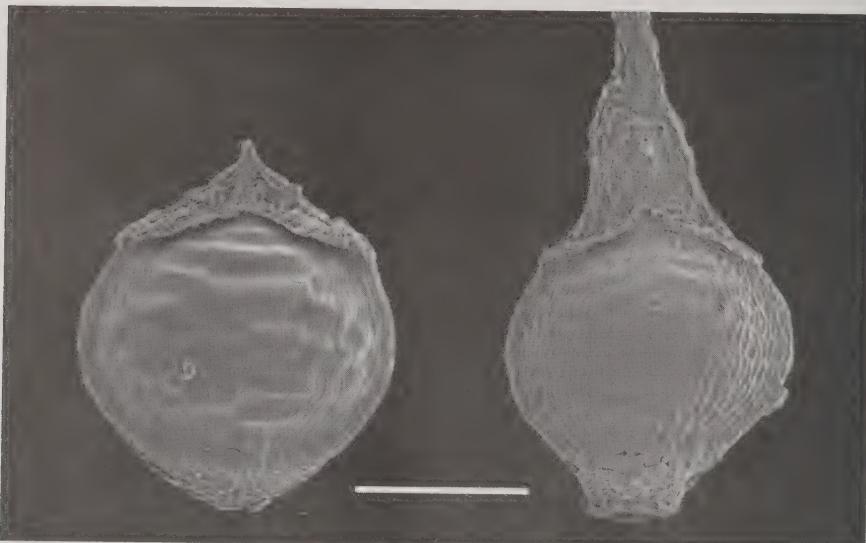


FIGURE 1. Achenes of *Rhynchospora nitens* (left) and *R. scirpoides* (right), from Reznicek 10966 and 10967 (MICH) respectively. The scale bar represents 0.5 mm.

discovery, ranging north to Oceana County, and although *R. scirpoides* was locally frequent in suitable habitats, no other stations for *R. nitens* were discovered.

Considerable searching, both in New England and in the Great Lakes region, has confirmed that the species is indeed very rare in the north, though one possible confounding factor in its recognition is similarity to the much more common and widespread *Rhynchospora scirpoides*. Superficially, these two species of generally similar habitat are essentially identical in appearance although, like Sorrie (1977), I noted that the spikelets of *R. nitens* had a subtle greyish cast to them (caused by a wider hyaline margin to the scale apices) that helped differentiate them from the dark brown spikelets of *R. scirpoides*. However, a quick examination of the achene tubercles will easily separate the two species. The tubercles of *R. nitens* are short, less than 0.5 mm long, distinctly broader than long, and abruptly contracted into the promptly deciduous style. Those of *R. scirpoides* are much longer, conspicuously longer than wide, and gradually tapered into the more or less persistent style. These differences are visible in the field with the naked eye or a low power hand lens. The achenes of *R. nitens* are also strongly transversely rugose, much more so than the nearly smooth achenes of *R. scirpoides* (Fig. 1). When they are just reaching maturity, the achenes of *R. scirpoides* also show a conspicuous pale border that is absent on the achenes of *R. nitens*.

SPECIMEN CITATION

MICHIGAN. ALLEGAN Co.: Allegan State Game Area, Goose Lake, N of 130 Ave. and W of 38th St., SE $\frac{1}{4}$ section 14, T3N R14W, ca 8 mi. NNW of Allegan. A.A. Reznicek 10966, F.W. Case, M. Penskar, 18 August 1999. (GH, MICH, MSC, NY, US, VDB, WIS).

ACKNOWLEDGMENTS

I am grateful to Fred Case and Mike Penskar for joining me in the field and helping look for these coastal plain disjuncts. I am also grateful to Bev Walters for taking the achene SEM photos.

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ANNOUNCEMENT

Checklist of the Vascular Plants of Wisconsin. July, 2001. The Wisconsin Department of Natural Resources and the University of Wisconsin-Madison Herbarium announce the publication of this volume, authored by Mark A. Wetter, Theodore S. Cochrane, Merel R. Black, Hugh H. Iltis, and Paul E. Berry and available at no cost from the Wisconsin DNR, Technical Bulletin No. 192, paperback. For a free copy, contact the Bureau of Integrated Science Services Research Center, 1350 Femrite Drive, Monona, WI 53716. Telephone 608. 221. 6320; fax 608. 221. 6353.

NOTEWORTHY COLLECTIONS

MINNESOTA

DIGITALIS GRANDIFLORA Miller (Scrophulariaceae). Yellow Foxglove.

Previous knowledge. *Digitalis grandiflora* is a biennial or perennial native to Eurasia, where it grows in woods (Tutin et al. 1972). In eastern North America, *D. grandiflora* occasionally escapes from cultivation (Magee & Ahles 1999). *D. grandiflora* has been reported outside of cultivation from Baraga and Houghton Counties in upper Michigan (Voss 1996). We are not aware of other collections from the upper Great Lakes.

Significance. A population of *D. grandiflora* was found in Duluth, Minnesota, apparently the first escape of this species in the state. The plants were on a steep, open northeast-facing bank about 1 km from Lake Superior. This is a residential neighborhood, in which the population's founders may have been cultivated. The species was absent from a similar bank across the avenue, suggesting that spread by seed is weak. The plants had large rhizomes bearing numerous scars from flowering stems, and have been observed flowering vigorously every year since their discovery. We infer that *D. grandiflora* behaves as a perennial in this environment, allowing it to persist and spread locally even if reproduction by seed is ineffective. This species contains some of the same cardiac glycosides as *D. lanata* Ehrh. and *D. purpurea* L. (Hollman 1985), suggesting that caution be taken to prevent skin contact or ingestion by humans, livestock, or pets.

MINNESOTA. ST. LOUIS CO.: narrow patch about 12 m long between sidewalk and overgrown lot, plants in flower, with *Campanula rapunculoides* L., SW side of 24th Ave. E above Superior St., Duluth, NW $\frac{1}{4}$ SW $\frac{1}{4}$ Sec. 13, T50N, R14W, 22 Jul 1997, Walton 2542 (DUL, MIN).

ELAEAGNUS COMMUTATA Bernh. (Elaeagnaceae). Silver-berry.

Previous knowledge. *Elaeagnus commutata* is a shrub to small tree native to Canada and northern United States (Gleason & Cronquist 1991). Its native range in Minnesota is confined to the northwestern counties (Ownbey & Morley 1991). Plants have been collected about 50 km west of Thunder Bay, Ontario, Hartley 238 (LKHD), and on the Lake Superior shore in Pukaskwa National Park, Ontario, Garton & Smits 17704 (LKHD).

Significance. Numerous young stems of *E. commutata* were growing in ballast throughout about 30 m of railroad in Duluth, Minnesota, a line that has not had traffic for several years. The presumed parent was a fruiting clump with stems up to 2.5 m tall, which existed a few meters from trackside. Also, thousands of stems from a few cm to 1.5 m tall were found on a steep Mesabi Iron Range (Minnesota) mine dump in gaps in a plantation of *Pinus resinosa* Ait. and *P. banksiana* Lamb., with which *E. commutata* was planted for reclamation in the 1970s. *E. commutata*, a nitrogen-fixing species (Visser et al. 1990), has been planted for revegetation of poor soils. It could not be found in apparently suitable open habitats that adjoined this pine plantation. These seem to be the first reports of local spread by this species outside of its native range in the Great

Lakes area, some 200–250 km from the nearest known native range limit. The Duluth site is about 3 km from similar habitat in Wisconsin.

MINNESOTA. ST. LOUIS CO.: plant in flower and fruit, mixed-species thicket in waste ground near railroad, between 41st & 42nd Aves. W below Grand Ave., Duluth, NW $\frac{1}{4}$ NW $\frac{1}{4}$ Sec. 8, T49N, R14W, 6 Jul 1999, Schimpf & Newman 273 (DUL); plants in flower, gaps in pine plantation, S end of W slope of mine surface overburden dump just S of Mountain Iron, SW $\frac{1}{4}$ NE $\frac{1}{4}$ Sec. 9, T58N, R18W, 10 Jun 2000, Schimpf 281 (DUL, MIN).

***FILAGO ARVENSIS* L. (Asteraceae).** Field Filago.

Previous knowledge. *Filago arvensis* is a European annual that has seldom been collected in the eastern United States (Gleason & Cronquist 1991). In the upper Great Lakes area the only reported populations are from northern lower Michigan, from which there are no collections in recent decades (Voss 1996), and Manitoulin Island, Ontario, in Lake Huron (Scoggan 1979).

Significance. This is apparently the first record for Minnesota; it represents several hundred plants at a remote site in the Superior National Forest, where it was associated with many other short-lived weedy species. Some heads were still in flower, while others had dispersed fruit.

MINNESOTA. ST. LOUIS CO.: in full sun on dry gravel and sand of recent logging trail, SW $\frac{1}{4}$ SE $\frac{1}{4}$ Sec. 19, T59N, R13W, 25 Aug 1998, Walton 3338 (DUL).

***GERANIUM ROBERTIANUM* L. (Geraniaceae).** Herb Robert.

Previous knowledge. *Geranium robertianum* is an annual or biennial considered by some (e.g., Voss 1985) to be native to eastern North America, and is clearly native to much of the Palearctic region (Tutin et al. 1968). The populations closest to Minnesota appear to be in eastern upper Michigan (Voss 1985), the Door Peninsula of Wisconsin (Wisconsin State Herbarium 1999), and the southern reaches of northwestern Ontario (Scoggan 1978).

Significance. This is apparently the first report for Minnesota. The extent of occurrence was limited, so that wider naturalization in the state is far from certain. Plants were in flower and fruit.

MINNESOTA. ST. LOUIS CO.: common in a shady bed where *Convallaria majalis* L. is cultivated, along foundation on E side of residence, Duluth, plants to 60 cm, stem bases red, NW $\frac{1}{4}$ SE $\frac{1}{4}$ Sec. 7, T50N, R13W, 26 Jul 1999, Schimpf & Newman 277 (DUL, MIN).

***LEUCANTHEMELLA SEROTINA* (L.) Tsvelev (Asteraceae).** Giant Daisy.

Previous knowledge. *Leucanthemella serotina* is a tall perennial native to wet habitats in southeastern Europe (Tutin et al. 1976). It has been collected infrequently outside of cultivation in the northeastern U.S. The collections closest to Minnesota are from Iron County, Michigan (Voss 1996) and Douglas County, Wisconsin (Wisconsin State Herbarium 1999).

Significance. This is apparently the first collection for Minnesota. The plants grew at the upland edge of a wetland of the lower St. Louis River, which is subject to water-level fluctuations driven by seiches in Lake Superior. Stortz & Sydor (1980) found typical within-day changes in water level to be at least 15 cm at an open-water measurement point about 6 km downstream from this collection site.

Neighboring species were *Typha latifolia* L., *Calamagrostis canadensis* (Michx.) P. Beauv., *Carex lacustris* Willd. and *C. lasiocarpa* Ehrh., *Lythrum salicaria* L., *Potentilla palustris* (L.) Scop., *Aster borealis* Prov., and *Cicuta bulbifera* L.

MINNESOTA. ST. LOUIS CO.: a single clump covering about 0.3 m², junction of steep slope with wetland just S of Oliver Bridge, Duluth, plants in flower and with mature seeds, SW $\frac{1}{4}$ NE $\frac{1}{4}$ Sec. 11, T48N, R15W, 19 Oct 1999, Walton 3947 (DUL).

POA BULBOSA L. (Poaceae). Bulbous Bluegrass.

Previous knowledge. *Poa bulbosa* is a viviparous weedy perennial native to Eurasia (Tutin et al. 1976). Although Minnesota is one of few states from which it has not been reported (USDA, NRCS 1999), the species is much less common in eastern than in western North America (Gleason & Cronquist 1991). This is likely due to the propensity of the plants to aestivate (Ofir & Kigel 1999) while summer-active competitors can take advantage of frequent rain.

Significance. This is apparently the first report for Minnesota, only some 20 km from North Dakota. At the time of collection plants had aestivated and those still bearing bulblets in "infructescences" could be found only where fixed objects had protected them from mowing. *P. bulbosa* had been observed in active growth on 16 May 1999 widely spread over about 2 ha of maintained turf at the same site, but purplish bulblets had not yet become evident.

MINNESOTA. CLAY CO.: turf of general public campground, Buffalo River State Park, with scattered deciduous trees, SE $\frac{1}{4}$ Sec. 10, T139N, R46W, 13 Jul 1999, Schimpf 270 (DUL).

SCROPHULARIA NODOSA L. (Scrophulariaceae). Woodland Figwort.

Previous knowledge. *Scrophularia nodosa* is a perennial native to woods in most of Europe (Tutin et al. 1972). It has been sparingly cultivated in North America, and a few escapes have been reported for New England (Gleason & Cronquist 1991, Magee & Ahles 1999). This species seems not to have been reported for the upper Great Lakes area.

Significance. This is apparently the first report for Minnesota. Two small patches were found on opposite sides of the same small tributary to Lake Superior, in moist clay soil under deciduous trees in a community containing both native and naturalized species. A third small patch was seen about one block downstream from the collection site. The surrounding area is residential, and the site is about 250 m from the lakeshore. The plants were flowering and fruiting. The rhizomes are conspicuously nodular, petioles of the principal leaves are about 1/4 the length of their laminas, petals have green tips, and the staminode is dark brown and about as long as wide. These character states separate these plants from *S. marilandica* L.

MINNESOTA. ST. LOUIS CO.: creek bank above London Rd. at 39th Ave. E, Duluth, NW $\frac{1}{4}$ NW $\frac{1}{4}$ Sec. 18, T50N, R13W, 18 Sept 1997, Walton & Newman 2684 (DUL, MIN).

SENECIO VULGARIS L. (Asteraceae). Common Groundsel.

Previous knowledge. *Senecio vulgaris* is an annual from Eurasia that is widely naturalized in North America. Fernald (1950) lists flowering as early as March,

Gleason & Cronquist (1991) as early as May. All nine previous Minnesota collections in DUL & MIN were taken in flower from June through October.

Significance. Individuals were collected in flower in Duluth, Minnesota, as early as April after extremely mild winters in recent years. This suggests that this species may behave as a winter annual, or less likely as a biennial, and flower early where microclimate is warmed near buildings. The population did not fruit until May. These plants are shorter and more tomentose than summer or autumn collections in DUL.

MINNESOTA. ST. LOUIS CO.: cultivated deciduous shrub bed with bark-chip surface about 1 m from SE side Heller Hall, University of Minnesota, Duluth, center NW $\frac{1}{4}$ Sec. 14, T50N, R14W, 27 Apr 1998, Schimpf 269 (DUL); same location, but about 2 m from building, 22 Apr 2000, Schimpf 279 (DUL).

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THE BIG TREES OF MICHIGAN

24. *Taxodium distichum* (L.) Richard

Bald Cypress

Dave Dehn and Elwood B. Ehrle

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The largest known Bald Cypress in Michigan is located in the Kleinstuck Preserve in Kalamazoo, Kalamazoo County, Michigan, in the southwest portion of the lower peninsula.

Description of the species: The Bald Cypress is a member of the family Taxodiaceae, along with the Sequoias. (Modern opinion mostly favors merging the Taxodiaceae into the Cupressaceae, as was done in volume 2 of *Flora of North America*, 1993.) The genus *Taxodium* is distinguished from other members of the family by its flattened, deciduous needles (Fig. 1). The leaves are two-ranked, and many times, entire leafy branchlets are shed as a unit. The seeds are three-angled and there are two seeds borne on the upper surface of each cone scale. *Taxodium distichum* is predominantly southeastern in its distribution, but extends west to Texas and Mexico, and north as far as Maryland and Long Island, NY, and it reaches the lower Ohio River and even grows along the Wabash River on the Illinois-Indiana border.

The Michigan State Champion Bald Cypress was planted around 1855 by Carl G. Kleinstuck when the area was known as Bragg's Nursery. The tree is, therefore, about 145 years old.

Location of Michigan's Big Tree: Michigan's largest known Bald Cypress can be found in the city of Kalamazoo. The tree can be reached by taking Maple St. to Stearns Ave., about 100 yards past the YMCA. Take Stearns Ave. one block to its end at the entrance to the Kleinstuck Preserve. Follow the trail from the end of Stearns Ave. a short distance over a hill and through a 1940s pine plantation. Follow the trail down a slope to the circle trail that goes around the wet depression in the center of the preserve. Take the trail to the right a short distance around the north side of the wet depression. The trail passes over a drainage ditch about 25 yds. before the tree. The tree is easily visible, and is 3 yds. off the south side of the trail. The map coordinates for this location are T2S, R11W, section 28.

Description of Michigan's Big Tree: The tree has a healthy, solid trunk. One branch emerges about 5' from the ground; under the branch there is a wood-pecker hole. The circumference of the tree at breast height was measured on 12

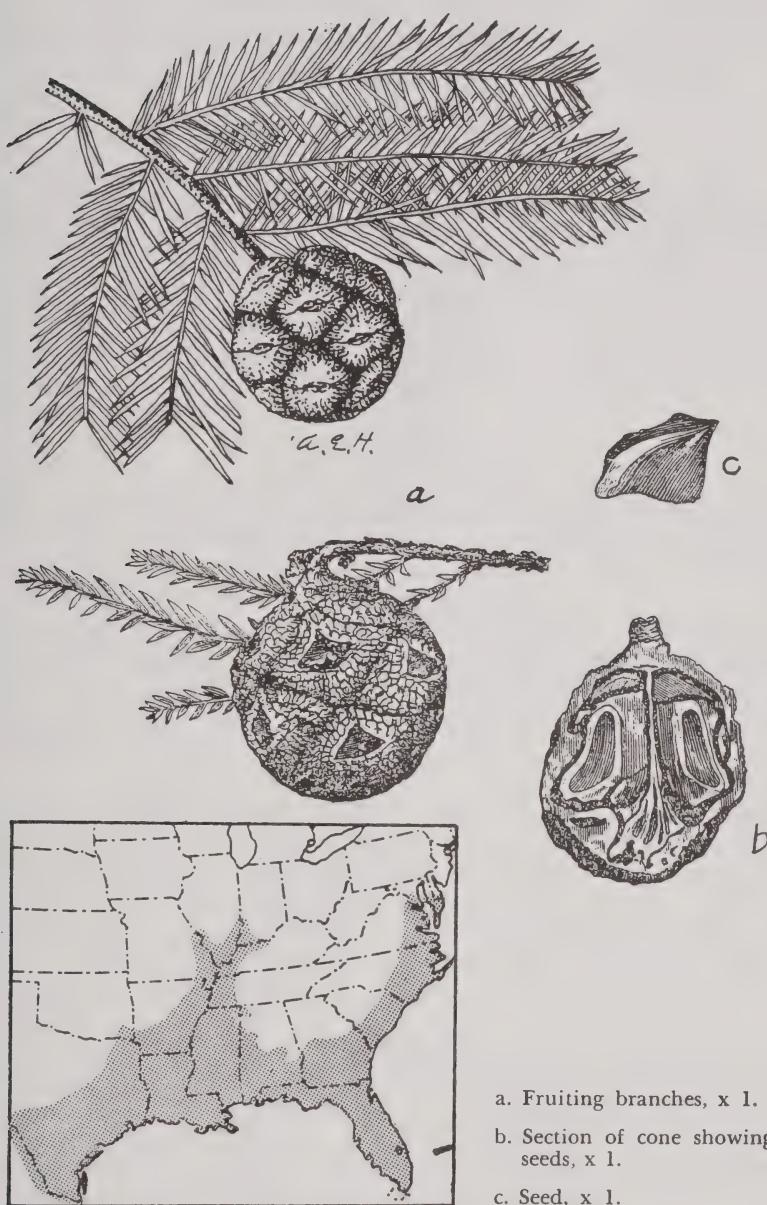


FIGURE 1. Characteristics of the Bald Cypress. The illustration is reproduced from Preston, 1976, p. 92, and used with permission.

April 1996 by D. Dehn, E. Ehrle, and A. Goddard at 116" (295 cm). The crown spread was measured at 31' (10 m). The height was measured at 68' (21 m).

INVITATION TO PARTICIPATE

If you would like to join us in extending this series of articles by visiting and describing one or more of Michigan's Big Trees, please contact Elwood B. Ehrle for help with locations, specifications for taking measurements, and assistance with the manuscript. The Michigan Botanical Club encourages your involvement in this activity. Please remember to ask permission before entering private property.

DEDICATION

This series of articles is dedicated to the memory of Paul Thompson, Michigan's Big Tree Coordinator for over 40 years, who died in 1994.

LITERATURE CITED

Preston, Richard J. 1976. North American Trees. Iowa State University Press, xxix + 399 pp. Ames, Iowa.

THE BIG TREES OF MICHIGAN

25. *Sequoiadendron giganteum* (Lindl.) Buchholz
Giant Sequoia

Bonnie B. Harnish, Chair

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Manistee, MI 49960

Elwood B. Ehrle

Department of Biological Sciences
Western Michigan University
Kalamazoo, MI 49008

Michigan's largest known Giant Sequoia stands on the grounds of the Lake Bluff Audubon Center near Manistee, Manistee County, MI, on the western side of the lower peninsula.

Description of the Species: The Giant Sequoia is a member of the Taxodiaceae, along with the Bald Cypress. (Modern opinion mostly favors merging the Taxodiaceae into the Cupressaceae, as was done in volume 2 of *Flora of North America*, 1993.) The genus *Sequoiadendron* is distinguished from other members of the family by having leaves which are scale like. They are hard and prickly and give the branchlets a cord-like appearance (Fig. 1). The dark reddish-brown, ovoid cones are 2–3.5" long and 1.5–2" broad. *Sequoiadendron giganteum* is native in a small portion of the Sierra Nevada of California. The Michigan State Champion Giant Sequoia was planted as 2–3 year-old seedling in 1949. The tree is therefore just over 50 years old.

Location of Michigan's Big Tree: The tree is located on the grounds of the Lake Bluff Audubon Center near Manistee, Michigan. To reach the tree, take U.S. Route 31 north from Manistee. Where MI Route 110 turns to the left and U.S. Route 31 continues to the northeast, turn left onto MI Route 110. The Lake Bluff Audubon Center is on MI Route 110, 1.8 miles from its junction with U.S. Route 31. The tree is approximately 250' south of the headquarters building of the Lake Bluff Audubon Center.

Description of Michigan's Big Tree: The tree is magnificent and has a healthy, solid trunk. It is beautifully symmetrical with a gradually tapering conical shape. It was measured on 26 July 1995 by the authors. Its girth is 151" (3.83 m). It is 58' (17.7 m) tall and has a crown spread of 30' (9.1 m). Its rapid growth rate is indicated its having reached this size in only 50 years and its increase in girth by 13" and in height by 11' since it was last measured (date unknown) by P. Dakin, G. Terry, and R. Spenski.

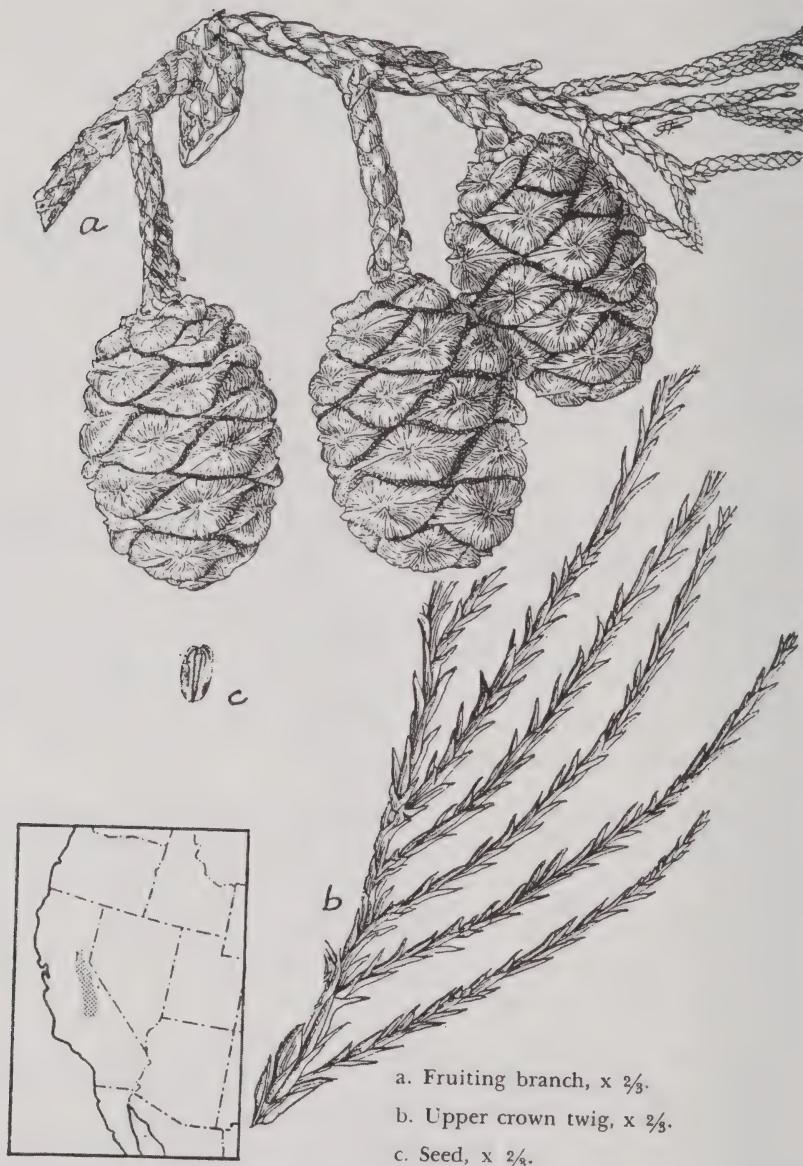


FIGURE 1. Characteristics of the Giant Sequoia. The illustration is reproduced from Preston, 1976, p. 90, and used with permission.

INVITATION TO PARTICIPATE

If you would like to join us in extending this series of articles by visiting and describing one or more of Michigan's Big Trees, please contact Elwood B. Ehrle for help with locations, specifications for taking measurements, and assistance with the manuscript. The Michigan Botanical Club encourages your involvement in this activity. Please remember to ask permission before entering private property.

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On the cover: *Pawpaw*, *Asimina triloba* (L.) Dunal. *The flower* is 3—4 cm broad. *Photographed along the Olentangy River, Columbus, Franklin County, Ohio, 8 May 1987, and reproduced here by courtesy of Thomas G. Lammers, UW-Oshkosh, 54901.*

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THE

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October, 1999



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NEW LOCALITIES FOR *BUELLIA NIGRA* IN MINNESOTA AND THE FIRST REPORT OF THIS CRUSTOSE LICHEN FROM SOUTH DAKOTA

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ABSTRACT

Eighteen new localities in Minnesota are reported for *Buellia nigra*, a crustose lichen previously known from only three sites in North America. Most new collections come from granite and gneiss outcrops and boulders situated along the western half of the Minnesota River valley, and one additional record comes from the northeastern arm of the river; the remaining collections come from quartzite outcrops and boulder-strewn moraines in southwestern Minnesota. Additionally, this note represents the first report of this species from South Dakota.

In 1997, a three-year study was initiated by the Minnesota County Biological Survey (MCBS) to investigate sites of botanical interest in sixteen counties bordering the Minnesota River in southern Minnesota. The MCBS is a project of the Minnesota Department of Natural Resources. The goal of the MCBS is to identify significant natural areas and to collect and interpret data on the distribution and ecology of rare plants, rare animals, and native plant communities. Among the most noteworthy collections made during this study are those of the crustose lichen *Buellia nigra* (Fink) Sheard. Lichen nomenclature throughout the paper follows Esslinger & Egan (1995). All collections of *B. nigra* cited at the end of this report are those of the author and will eventually be deposited at the University of Minnesota Herbarium (MIN), with duplicate specimens being sent to various herbaria.

Prior to the 1997–99 survey, *Buellia nigra* was known from only three sites in North America (Fink 1902; Sheard 1969; Wetmore 1988), two in Minnesota and one in North Dakota. The type collection (Fink 146, holotype: *non vidi*; Fink 153, “topotype”: MIN), made in 1900, comes from near Battle Lake in Ottertail County, Minnesota. Although this North American endemic was described in 1902 (as *Rinodina nigra* Fink), it was not collected again until 1908, when it was discovered in La Moure County, North Dakota (Brenkle 1781, FH). Notably, both of these early collections come from glacial erratic boulders on moraines. A third site for the species was discovered in 1978 in Winona County, Minnesota

*Requests for reprints should be sent to this address.



FIGURE 1. Distribution of *Buellia nigra* in North America.

(Brako 1293 and 1300B, MIN), where it was collected on chert but apparently is rare at that locality. In addition to eighteen new Minnesota sites discovered for this species during the 1997–99 survey (see Fig. 1 and citations given further below), a collection of *B. nigra* was also made in eastern South Dakota, the first from that state.

Buellia nigra is characterized by having a thin, brown-colored thallus and by giving negative thalline reactions. These characters separate it from the similar-appearing species, *B. aethalea* (Ach.) Th. Fr., which has a potassium hydroxide-positive red thallus and slightly larger spores (Wetmore 1988, p. 236). The distinctive brownish thallus of *B. nigra* is regularly areolate, with areolae up to 0.6 mm wide, though the average width is about 0.4 mm. The majority of areolae bear apothecia, with the latter being innate, up to 0.3 mm in diameter and having a margin confluent with the black epruinose disc (Sheard 1969). Also, the hypothecium (layer below the spore-bearing layer in the fruiting body) is hyaline, the spores are brown, one-septate, and 9 to 12 by 5 to 9 micrometers (Wetmore 1988, p. 236).

Before the 1997–99 survey, *Buellia nigra*, which is listed as State Endangered in Minnesota (Wetmore 1988), had been collected on granite and chert but little else was known about the species. The recent discovery of this lichen in south-central and southwestern Minnesota, however, is leading to a better understanding of its distribution and ecology. At the twelve new sites along the NW-SE arm of the Minnesota River (Fig. 1), the species is abundant only at the Morton outcrops, but even there it seemingly occurs in only the southwestern portion of the site, where hundreds of small patches of *B. nigra* grow on the flat surface of gneiss outcrops as well as on adjacent boulders. At the other sites along the river, the species is rare to occasional on gneiss and granite boulders. For instance,

only a few small patches of *B. nigra* were observed on boulders at the Gneiss Outcrops Scientific Natural Area (SNA), where the first collection of this species in 1997 was made. Away from the river, *B. nigra* was collected on glacial erratic boulders near the summit of a boulder-strewn moraine in Yellow Medicine County (Wheeler 18580), though again only a few patches were observed. In Pipestone and Rock counties, in extreme southwestern Minnesota, *B. nigra* occurs on Sioux Quartzite, which is a metamorphosed, pinkish-red quartz sandstone that is extremely hard (Ojakangas & Matsch 1982). It is noteworthy that the population of *B. nigra* at Blue Mounds State Park in Rock County is the largest discovered to date. No collection of the species was made at Blue Mounds State Park, but its known occurrence there is mapped in Fig. 1. The South Dakota collection (Wheeler 18600) comes from granitic boulders atop a boulder-strewn moraine. Further searches on boulder-strewn moraines in eastern South Dakota would very likely yield additional records of this species.

Whereas the western portion of the Minnesota River valley is bordered primarily by igneous and metamorphic rock outcrops, the NE arm of the river is bordered by dolomite and sandstone bluffs (Ojakangas & Matsch 1982). Scattered glacial erratic boulders do occur, however, on the remnant prairies that border the northeastern arm of the river. Although *Buellia nigra* was not observed on sedimentary rocks along the NE arm of the river, the species does occur at the Kasota Prairie in LeSueur County, where it is rare on granitic boulders. Also, *B. nigra* was not observed during a fortnight survey of crystalline rock outcrops in central Minnesota (Stearns and Benton counties) in July, 1997. Moreover, it seems to be absent from crystalline rock outcrops in northern Minnesota, a region relatively well searched for lichens.

Sheard (1969, p. 222) stated that *Buellia nigra* is often associated with *B. punctata* (Hoffm.) Mass. [*Amandinea punctata* (Hoffm.) Coppins & Scheid.], but this is not the case in south-central or southwestern Minnesota, where it is most often associated with *Aspicilia cinerea* (L.) Köber, *Candelariella vittelina* (Hoffm.) Müll. Arg., *Dimelaena oreina* (Ach.) Norman, *Lecanora muralis* (Schreber) Rabenh., *Physcia subtilis* Degel., *Pleopsidium flavum* (Bellardi) Körber and, less commonly, *Caloplaca flavovirescens* (Wulff) Dalla Torre & Sarnth., *C. sideritis* (Tuck.) Zahlbr., and *Melanelia tominii* (Oksner) Essl. The brownish thallus of *Buellia nigra*, however, can easily be confused, at a distance, with that of other species, such as *Acarospora americana* H. Magn. and *A. fusca* (Schrader) Arnold. It is also worth noting that *Pleopsidium flavum*, which has a bright lemon-yellow thallus and thus is one of our most distinctive lichens, is useful as an indicator species when searching for *B. nigra* in southern and western Minnesota.

Thalline patches of *Buellia nigra* range from (3-)10–30 mm broad (Figs. 2, 3). When present, this species typically covers less than 0.5 percent of boulder surface area, whereas more common species, such as *Aspicilia cinerea*, *Dimelaena oreina*, and *Pleopsidium flavum*, can each cover as much as 25 percent or more. But as intimated earlier, the percentage of boulder surface area covered by *B. nigra* at Blue Mounds State Park, as well as at the Morton outcrops, is appreciably higher than 0.5 percent. Indeed, at the former site, on some flat, outcrop surfaces the percentage of *B. nigra* cover reaches 1–3%. Relevé data for lichen

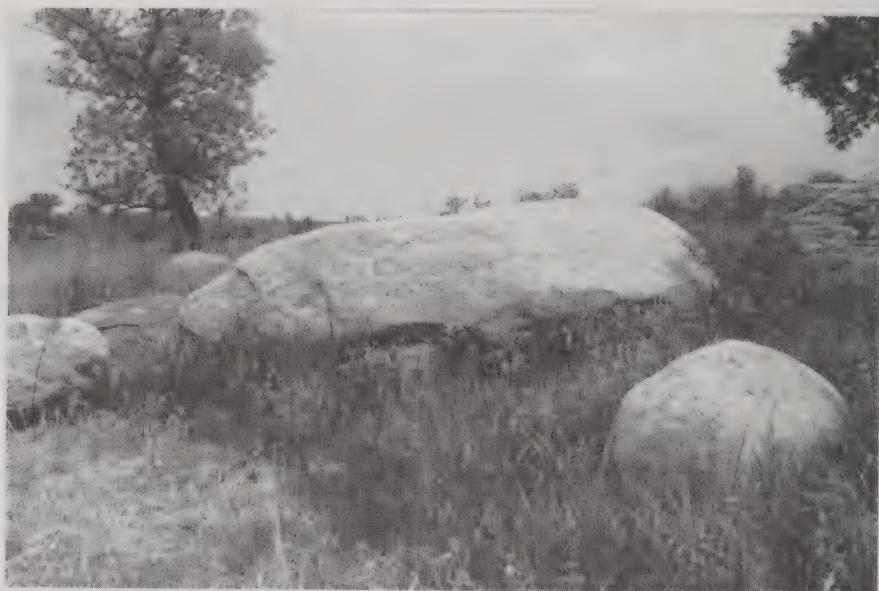


FIGURE 2. Granite outcrop in the Minnesota River valley below Ortonville. Dark patches of *Buellia nigra*, with southwest exposure, are evident on the largest boulder. Lichen dominants include *Dimelaena oreina*, *Lecanora muralis*, and *Pleopsidium flavum*. Big Stone Wildlife Refuge, 19 May 1999.

species and bryophytes associated with *B. nigra* at Blue Mounds State Park, and their cover values, are given in Table 1. (The relevé method, which was developed by the Braun-Blanquet school of phytosociology, is used to describe and classify vegetation within a study area. Visual estimates of cover-abundance, on a 5-point scale, are made for each species occurring within a plot. The relevé has been adopted by the Minnesota County Biological Survey as the major method for describing plant communities.)

All 1997–99 collections of this lichen were made on gneiss, granite, or quartzite and generally in partial or full sunlight. This presumed heliophyte generally grows on surfaces having south or southwest exposure, and most often it occurs on protuberant edges at or near the tops of outcrops or boulders. As *B. nigra* grows primarily in dry and sunny rocky areas, not surprisingly it is often associated with well-known pioneer lichen species, such as *Aspicilia cinerea* and *Dimelaena oreina*.

In conclusion, *Buellia nigra* is a saxicolous species that appears to be restricted to xeric surfaces of crystalline rocks in the eastern edge of the northern Great Plains. Besides being uncommon to only occasional at most sites, *B. nigra* has a very limited geographic distribution in North America, with seemingly a center of distribution in south-central and southwestern Minnesota. Due to its apparent rarity and restricted distribution, it is suggested here that following the retreat of the glaciers, approximately 13,000 years ago, *B. nigra* became isolated from a congener as the climate became warmer and the former species became



FIGURE 3. Closer view of the dark patches of *Buellia nigra* shown in Fig. 2. The center patch is about 25 mm broad. Big Stone Wildlife Refuge, 19 May 1999.

adapted to xeric conditions. Regarding a possible congener, Sheard (1969) claims that *B. nigra* is closely related to *B. aethalea*, with its spores being in the lower range of the latter species. It is noteworthy that *B. nigra* was not reported from the Black Hills of South Dakota (Wetmore 1968), though the similar-appearing and presumably closely related *B. aethalea* has been recorded from there.

MINNESOTA. BIG STONE CO.: E $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$ Sec. 27, T121N, R46W, ca. 2 mi. SE of Ortonville on Rte. 75, Big Stone National Wildlife Refuge, 5 May 1998, 18506. BROWN CO.: NE $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 19, T112N, R33W, ca. 15 mi. NW of Sleepy Eye, Morgan Sportsman Club Recreation Area, 18 May 1998, 18606. CHIPPEWA CO.: SW $\frac{1}{4}$, NW $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 12, T115N, R39W, Gneiss Outcrops SNA, ca. 2 mi. SE of Granite Falls, W of Pete's Pt. Rd. SE, 10 Aug 1997, 17075. LAC QUI PARLE CO.: S $\frac{1}{2}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 26, T121N, R46W, ca. 2.2 mi. SE of Ortonville, Big Stone Wildlife Refuge, 5 May 1998, 18481; SE $\frac{1}{4}$, SE $\frac{1}{4}$, NW $\frac{1}{4}$ Sec. 12, T120N, R45W, ca. 6 mi. NNE of Bellingham, 26 May 1998, 18771; SW $\frac{1}{4}$, NE $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 15, T120N, R45W, ca. 4.5 mi. N of Bellingham on Rte. 75, E of road, 26 May 1998, 18782. LE SUEUR CO.: SE $\frac{1}{4}$, NW $\frac{1}{4}$ Sec. 6, T109N, R26W, Ca. 1.5 mi. SW of Kasota, Kasota Prairie, 17 Jul 1999, 20108. NICOLLET CO.: NW $\frac{1}{4}$, SE $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 15, T111N, R32W, ca. 4 mi. SE of Fort Ridgely State Park on Rte. 21, 23 May 1998, 18718. PIPESTONE CO.: E $\frac{1}{4}$, SW $\frac{1}{4}$ Sec. 1, T107N, R46W, NW edge of Pipestone, Pipestone National Monument, 13 May 1999, 19544; N $\frac{1}{2}$, NW $\frac{1}{4}$ Sec. 1, T107N, R46W, NW edge of Pipestone, Hiawatha State Game Refuge, 14 May 1999, 19614. REDWOOD CO.: NW $\frac{1}{4}$, NW $\frac{1}{4}$, NW $\frac{1}{4}$ Sec. 11, T113N, R36W, Cedar Rock State WMA, ca. 3 mi. NE of Delhi, 2 Sep 1997, 17559; SW $\frac{1}{4}$, SW $\frac{1}{4}$, SE $\frac{1}{4}$ Sec. 15, T112N, R34W, ca. 6 mi. NNE of Morgan, 6 Sep 1997, 17794; NE $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$ Sec. 15, T112N, R34W, ca. 6.5 mi. N of Morgan, 23 Sep 1997, 17920. RENVILLE CO.: NW $\frac{1}{4}$, SW $\frac{1}{4}$, NW $\frac{1}{4}$ Sec. 31, T113N, R34W, Morton outcrop complex, W side of Morton, 5 Sep 1997,

TABLE 1. Relevé data from two quartzite outcrops in Blue Mounds State Park, each containing *Buellia nigra*; one relevé (each 2.5m × 2.5m) was made in the northern and the other in the southern end of the park.

Species	North	South
<i>Dimelaena oreina</i>	3	4
<i>Lecanora muralis</i>	1	2
<i>Rhizocarpon disporum</i>	2	1
<i>Physcia subtilis</i>	2	+
<i>Xanthoparmelia plittii</i>	2	+
<i>Aspicilia cinerea</i>	1	+
<i>Buellia nigra</i>	+	+
<i>Candelariella vitellina</i>	+	+
<i>Rhizoplaca subdiscrepans</i>	+	+
<i>Pleopsidium flavum</i>	—	+
<i>Acarospora americana/fuscata</i>	+	—
<i>Dermatocarpon miniatum</i>	+	—
<i>Grimmia laevigata</i>	+	—
<i>Hedwigia ciliata</i>	r	—
unidentified sterile crust	+	—

cover values: **r** (single occurrence); + (<5% – occasional); **1** (<5% – plentiful); **2** (5 – 25%); **3** (25 – 50%); **4** (50 – 75%); **5** (75 – 100%)

17697. ROCK CO.: S½, SE¼ Sec. 26, T104N, R46W, ca. 6.1 mi. W of Hardwick on Rte. 7, 15 May 1999, 19630. YELLOW MEDICINE CO.: SW¼, NW¼, NE¼ Sec. 4, T115N, R39W, Blue Devil Valley SNA, S side of Granite Falls, 3 Sep 1997, 17630; N½, NW¼, SE¼ Sec. 18, T115N, R46W, ca. 9.5 mi. NW of Canby, 9 May 1998, 18580.

SOUTH DAKOTA. DEUEL CO.: ca. 7.5 mi. W of Minnesota/South Dakota border on Rte. 22, S of road, 10 May 1998, 18600.

ACKNOWLEDGMENTS

The author thanks Clifford Wetmore for access to the lichen collections at the University of Minnesota Herbarium and also for verifying my identification of *Buellia nigra*; the curator of the Farlow Herbarium (FH), Harvard University, for information regarding Brenkle's collection from North Dakota; Tom Klein for the distribution map; and also Carmen Converse (MCBS supervisor) and Fred Harris (MCBS ecologist) for valuable comments on the manuscript as well as for their assistance and encouragement throughout the study.

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LABELING OF HERBARIUM SPECIMENS

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With interest strong (or required by law) in accurate identification of threatened, endangered, and otherwise protected plant species, not to mention general interest in our natural heritage, many individuals and agencies prepare specimens to submit for identification to herbaria and competent individuals. Such specimens can be important documentation for species occurrences, as well as valuable samples for persons studying particular species.

However, if these specimens are to fulfill their maximum potential, they must not only be good specimens but also be provided with good labels. Even if a collection has well-pressed flowers and fruit, not tangled in a large wad, possesses basal parts (rhizomes or roots), and displays both surfaces of leaves, it loses much of its value if the label says merely "Collected north of Lansing." After all, Sault Ste. Marie is north of Lansing! That extreme example of a vague label might have been satisfactory (or the best one could do) a century and a half ago. But modern criteria for a good label demand both more information and greater precision.

Few herbaria have an over-abundance of space for additional specimens, but most are glad to receive good ones, well-labeled, especially of interesting species or from under-collected regions. That is one way in which they augment their collections, and retention of desirable specimens is usually the only recompense expected in return for identification services. Skimpy little scraps of plants, with data scrawled on scratch paper, are less welcome (and likely to be discarded) for they provide nothing of much scientific value for further research or study—and, indeed, they may be so incomplete as to be unidentifiable.

Having examined and recorded data from approximately a quarter-million labels in the course of preparing text and maps for *Michigan Flora*, I feel somewhat prepared to offer advice. The outline following is intended to help in preparing truly useful and informative labels. Label information is sometimes even more valuable than the specimen itself. Only the collector knows fully the circumstances of collection, and thus bears responsibility for sharing (on the label) what he or she knows about the locality, habitat, appearance, and attributes of the plant—whatever cannot, years later, be determined from the pressed, dry carcass. The collector's original label, for better or for worse, is therefore carefully preserved with the specimen. Most herbaria do not have the staff to retype labels, even if they wanted to risk making errors in transcription from hastily scrawled data. Some people, unfortunately, write labels with no more concept of permanence than for a grocery shopping list, stringing together fragments of habitat and locality in random sequence, using obscure local names of places (in-

cluding roads, bars, fast-food establishments, etc.) that will very likely be unintelligible to anyone even a decade later.

When writing a label, the collector would do well to consider whether a botanist 100 or 200 years hence, perhaps on the other side of the continent, or even on the other side of the world, will be able to find the stated locality on a map and understand the observations recorded. That is just what we are now obliged to attempt with labels prepared in Michigan in the early to mid 19th century, often located at best only by farmers' woodlots or Indian names for landmarks. And it is why some of us collect old atlases, plat books, maps, railroad routes with listed stops, and such documents!

"Along road," a recent label says simply. That leaves lots of room for imagination. Was the plant in a weedy, bulldozed habitat? Was it in a natural situation? More instructive and precise statements, any of which could be true, might be "In wet roadside ditch at edge of cedar swamp"; "Border of beech-maple hardwoods next to dry gravel shoulder of road"; "Along a sandy two-track trail through clearcut surrounded by jack pine." Once collectors have gone to their reward (and I'd hesitate to suggest what that might be), they can no longer be questioned about flower color or pattern, fragrance of flowers or foliage, abundance, specialized habitat, kind of lakeshore, or other details that only they knew at the time of collection but failed to report on the label.

Even botanical beginners, still weak in their identification skills for difficult plants, can contribute valuably to science by preparing good labels. The specimens can be interpreted, and reinterpreted, later. The labels cannot. Hence this somewhat detailed account of points worth considering.

OUTLINE FOR PREPARING GOOD HERBARIUM LABELS

First of all, remember that the label prepared by the collector will remain with the specimen forever! If the information is copied to be more legible or is entered into a database, errors can occur in transcription. Therefore, the collector's original data are always preserved with the specimen for authenticity should questions arise.

- (1) Use high-quality materials: paper [acid-free] and ink [permanent, black waterproof]—not 3 × 5 cards. Trim label neat and square on the sides. (The label will be mounted, with the specimen, on heavy low-acid mounting paper.) [N.B.: Most herbaria prefer to mount specimens on their own paper (often pre-printed with official identification) and by their own chosen techniques. Avoid donating mounted specimens for identification unless you are assured that they will be welcome in that condition.]
- (2) Use common sense, e.g.,
 - (a) Keep the label compact. Long lists of associated species or other data belong in the collector's field notes or on *separate* memoranda, not all on a billboard label that leaves insufficient room for the specimen on a stan-

dard 11.5 × 16.5 inch sheet of herbarium paper. Furthermore, in databasing herbarium information, some older programs may not have allotted large enough fields to accommodate overly verbose label data.

- (b) Avoid wasting space identifying the fields of information. There is no need to write "Date" in front of what is obviously a date. Likewise, for "Name," "Habitat," etc. Just state the facts!
- (c) Similarly, there is no need to begin data with phrases like "Growing in . . ." or "Found in . . .". Obviously the specimen was found or it would not have been gathered. [A specimen collected where it was not found would be truly remarkable!] A specimen is ordinarily assumed to have been growing where it was found; if it was not (e.g., if it was blowing about in the wind, lying on the ground under a tree from which it fell, or washed up on the shore), that would be worth noting. Avoid needless words. Conserve space.
- (d) Be a severe proofreader. You will be embarrassed far into the future if labels bearing your name as collector have misspelled names of plants, localities, co-collectors, or other information. Double check the sources from which you copy. [It is depressing to see how many people appear incapable of copying names correctly out of the manual or flora that they used for reference!]
- (e) Be sure that units of measurement or parts described are indicated. "Abundance 1," "Height 15," "Color yellow" are not helpful statements without knowing the collector's code for abundance, the units in which height was measured, or the part that was yellow!

(3) Remember that your specimens, with their labels, may one day be included in a loan to Fort Worth, New York, Stockholm, Prague, Berlin, Warsaw, St. Petersburg, Beijing, Tokyo, or anywhere else in the world, for study by someone specializing in the family or genus. The language there may not be English or even use the English alphabet. Therefore, keep in mind:

- (a) Handwritten labels are often misread by other persons, sometimes leading to startling assertions of locality or habitat in published monographs, as well as misspelled names! Use a typewriter or computer to prepare absolutely legible labels. (Herbarium staff generally do not have the time or skill to copy accurately a diversity of poor penmanships from "temporary" labels! *Submit a good permanent label with each specimen.*)
- (b) Avoid all but the most obvious (preferably Latin) abbreviations. a.m. for a flower-opening time may be o.k., but U.S. postal abbreviations for states are not necessarily clear in the rest of the world (or even here, where MI means Michigan, not Minnesota, Missouri, or Mississippi). Short-cut abbreviations of plant names ["Q. vel." or "P. ser."] in habitat statements may mean nothing to persons in a part of the world where those plants (or names) are not known. M&NE, D & M, MDOT, R.W.W. will only confuse or perhaps amuse people in the next century.
- (c) The farther away the user is, the less likely he or she will understand the geography familiar to the collector or have detailed maps available. State and county should be clearly stated. Include a straight-line distance from

center of the nearest town (preferably in the same county, to avoid confusion in assigning localities). To benefit those with good maps, include an *objective* designation of locality, such as latitude and longitude (GPS can help) or section, range, and township in areas thus surveyed. The logical sequence is to understand “of”: SE $\frac{1}{4}$ NW $\frac{1}{4}$ sec. 15, T39N, R4W = SE $\frac{1}{4}$ of the NW $\frac{1}{4}$ of sec. 15 of T39N, R4W. But be sure the designations are accurate! [The Wisconsin collector who extrapolated that state’s meridian into the western Upper Peninsula of Michigan with “R15E” was really in R35W of the Michigan meridian—an error of some 300 miles.]

- (d) Further descriptions of locality may well be helpful *in addition* for local use, but avoid limiting locality data to ephemeral information like names of streets and highway route numbers (they shift over time!), property owners, commercial (or other) buildings, local nicknames for sites, etc. [A hundred years later, who will know where the edge of the K-Mart parking lot was, or the Cherry Hut, or the “Mudhole,” or “Potowatamie Road at end of pavement”? “Just southeast of Temporary Hwy. I-69 exit ramp . . .” was an only temporarily usable designation on one label!]
- (e) The label is ordinarily not the place for detailed *instructions* to reach a site. [As one label expressed it: “Enter a vacant lot between two houses. Travel S. through a cornfield, veer west, pass just S. of a sumac thicket.” The label that read “On right-hand side of Laird Road going east” could simply have said “S side of road.”]
- (f) Some sophisticated collectors have a small map printed on (or in the background of) their labels with the collecting site indicated. Such maps can be very helpful, but must indicate which direction is North. And the label should also make the locality clear *in words* that can be copied for citing in a monograph or entering in a database.

(4) Be sure to say something about abundance and the habitat as well as the locality. Herbarium specimens are not like stamps in a collection, simply filling vacancies in one’s holdings. They can be studied in their own right for anatomy, variation, and so forth. But additional information on the label can be invaluable. Whether the specimen was in a wet floodplain forest or a dry prairie, in waste ground or a bog, can affect its characters as well as help to understand the complexities of our natural world. [Careless collectors sometimes fail to clean the roots of their specimens, but such deplorable samples are another matter. Habitat should be stated on the label, not collected!] Some special points:

- (a) Make clear the conditions where the *specimen with the label* came from. “Multiple-choice” labels may fail to specify conditions where the specimen actually grew (and thus what situation might explain any variation from the norm for the species); better to say, e.g., “In wet ground . . .” and then add on the label “Also seen in dry ground . . .” The label (for a sand dune species) that said merely “near hemlock stand” would have been better if it had declared what habitat the plant was actually in. Labels that have some general printed indication like “Mosaic of red and

PLANTS OF MICHIGAN

COLLECTED FOR THE HERBARIUM OF THE UNIVERSITY OF MICHIGAN

Adenocaulon bicolor Hook.

ALGER CO.: ca. 2½ mi. SW of Grand Marais, stabilized dunes above N end of Grand Sable Lake. Rich Acer-Tsuga-Populus woods.

Flowers white. Crushed plant parts with spicy tomato odor. Plant glutinous.

Plants solitary, locally common.

ROGER W. SANDERS, NO. 60

12 July 1973

MICHIGAN NATURAL FEATURES INVENTORY — CAMP GRAYLING PROJECT
FLORA OF MICHIGANAgrostemma githago L.

KALKASKA Co.: N side of gravel road, 0.3 mile W of Sunset Trail and 3 miles S of Highway 72 (14 miles W of Grayling).

T26N, R06W, sec. 1, SE½ SW¼
Disturbed Mesic Northern Forest; along fence row in rye field.
Rare.

Petals deep purple w/ dark striations towards white center.
Associates: Berteroa incana; Secale cereale; Rumex acetosella;
Bromus inermis; Pteridium aquilinum.

Phyllis J. Higman 233

25 June 1993

University of Michigan Herbarium
FLORA OF MICHIGAN***Prunus persica* (L.) Batsch**

WASHTENAW Co.: Ann Arbor, 890 Wickfield Court.
Lat. & Long. 42° 18' 07" N 83° 43' 55" W

Rough, shrubby area along fence between two yards.
Single spontaneous small tree to 3 m, observed for several years, now flowering and fruiting; flowers (in spring) pale pink; fruits beginning to mature.

A.A. Reznicek 10666

JUN 21 1998

PLANTS OF MICHIGAN
HERBARIUM OF THE UNIVERSITY OF MICHIGAN

Calamintha arkansana

DELTA CO.: frequent, damp gravelly shore meadow along Lake Michigan S of Sucker Lake, NE1/4 sec. 24, T38N, R19W, ca. 5 mi. NE of Fairport.

Corolla magenta; bruised plant very aromatic.

E. G. Voss 16590
with Don Henson

September 4, 1997

SAMPLES. Reproduced here (much reduced) are a few actual labels, for the most part illustrating some of the practices recommended.

jack pine plantations and aspen clones. Steuben Lake has a wet wooded border, shore veg. includes cattails, bulrushes, pickerelweed and sedges" are useless for understanding the habitat of the specimen at hand, as is the brief "ditches and hills" with no word as to whether the single specimen came from a ditch or a hill! "Water varying from 0 to 1 m" does not say whether the specimen came from dry land. "Along shore and interior" on an island covers *everything*! The point of the label is not to report what the collector did all day, but where the particular specimen it accompanies occurred.

(b) For species that are known as cultivated plants, the label should indicate whether the collector thought the specimen was established outside of cultivation. A label that says "In Mrs. Smith's garden" does not make clear whether the collector recognized it as a weed in that garden, either a casual waif or well established, or planted. [In general, spontaneous weeds and escapes from cultivation, whether in a garden, farm, or cemetery, are likely to be included in a local flora, but plants growing where they were planted (either under glass or outdoors), are not. This kind of

problem has become increasingly important with the advent of seed mixes for restoring prairies or other habitats.] A label with some clue as to origin of possibly planted species is a blessing!

(c) Similarly, native plants at or near the edge of their range in the region where collected pose a problem that only the collector can readily address. For example, was a plant "along railroad," lacking further data, thought to be a waif in waste ground or a relic in a right-of-way strip prairie? Let the label offer some idea!

(5) Help the person using your collection by providing information (in addition to locality and habitat) not evident from the dried specimen.

(a) If it is not possible to gather the entire plant, including underground parts, the label should provide the missing information, e.g., "From [or, if true, beneath] a tree 1.2 m in diameter"; "much-branched shrub ca. 2 m tall"; "selected small specimen (others seen to 3 m tall)"; "larger leaves from root sprout"; "plant with extensive rhizomes."

(b) Flower color (especially blue) often fades to white or simply turns brown with time. Color of flower (more specifically, usually, of corolla) should be stated on the label, noting any spots, stripes, or other variation from uniform color. *It is frustrating to try to run something through a key that asks for color, when the collector failed to reveal what that was and it cannot be seen on the dry parts!* Furthermore, corolla color sometimes changes on drying to something other than white or brown. If the label says "Flowers purple or white" that doesn't reveal whether all specimens on the sheet were one or the other or, if mixed, which was which (nor, for that matter, what part of the flower was colored).

(c) Distinctive aroma (flower or crushed foliage?), white or colored sap, stinging hairs, glaucous surfaces, and such features should not be left to the imagination of one who consults the specimen years later.

(d) Anyone who has used keys to determine unknown plants knows that in some groups certain other information is needed that is often very difficult to ascertain from a pressed specimen, such as number and orientation of fertile stamens in a mint, number of styles in a pink, which violet petals (if any) are bearded. [Gathering, in the first place, of specimens with parts required for identification, like fruit in mustards and umbellifers and basal parts in many plants, is first of all the responsibility of the collector, not of the label per se.]

(6) Format:

(a) At the top of a label, a general heading may be appropriate, like "Plants of Superior County, Michigan" or "Herbarium of Sherlock Holmes Academy" or simply "Plants of Minnesota".

(b) Otherwise, the scientific name of the plant (or blank space for it) should be placed conspicuously at the top of the label, as that is how the specimen will ultimately be filed.

(c) Next (below the name) come the locality and habitat, in some logical arrangement but preferably separable. Certainly the state (if not in a

heading) must be included. It is helpful to have the county displayed in capital letters as a major category. There are many cities with the same name in different states, and numerous counties with townships of the same name within a state (e.g., Burt, Van Buren, Clinton, Lake, Superior in Michigan).

- (d) Then additional notes (see section 5 above). [Lack of clear distinction between different kinds of information can lead to such confusion as "Laxly Caespitose, Canada" cited as a locality in a foreign journal!]
- (e) At the bottom of the label belong the collector and number. These do belong *together*, the number *immediately following the name*, not somewhere else on the label. The easiest and least ambiguous numbering system is to start with simple number 1 and keep going the rest of your life. Trying to incorporate part of the date and/or locality, renumbering from 1 every year or in different regions or for different groups of plants, adding prefixes, or other schemes can lead to confusion in the future. Duplicates, i.e., all plants of the same kind from the same individual (woody or otherwise large) or uniform colony (herbaceous) *on the same date* should all receive exactly identical numbers, not supplemented with additional digits or codes. The collector's name and number (e.g., *Farwell 5944*) are forever linked to designate a particular collection and its duplicates (it is therefore redundant to incorporate collector's initials in a numbering scheme). Persons reporting on specimens sent for identification will use the collector/number designation. If a tall specimen was too large to press for one sheet, but was divided into two or more sheets, then identical labels should be provided for each sheet (and can be labeled "sheet 1," "sheet 2," etc.) If a gathering was inadvertently mixed when numbers were assigned in the field, the original number can be retained for both collections after separation, with a letter after it (or at least after one of them), e.g., 14396A and 14396B.
- (f) In the date, be sure to give all four digits for the year and write out the month. Many people around the world use different sequences, and shortening the date can lead to error. Material (e.g., fruiting) collected on a later date from the same colony or individual should bear a new collection number, but a reference to the other number and date is helpful.

CAVEAT

The advice offered here is intended primarily for collectors of vascular plants in the temperate Great Lakes region of North America, not necessarily for those in other regions of the continent or world, where factors such as elevation, use by indigenous peoples, or aboriginal (vernacular) names are also important to record on labels. The herbarium practices assumed are generally followed worldwide but derive specifically from the University of Michigan Herbarium. A collector whose specimens are to reside in a particular herbarium should of course follow any practices preferred by that institution.

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On the cover: *Wild Strawberry*, *Fragaria virginiana* Duchesne.

Along Indian Creek, Reily Township, Butler County, Ohio, 14 May 1989,
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